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A new species of *Sphenocarcinus* A. Milne Edwards, 1875 from tasmantid guyots, *S. lowryi* n.sp. (Crustacea: Decapoda: Brachyura) with notes on the taxonomic status of the genus ..... Bertrand Richer de Forges 1

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Records of the Australian Museum (1992) Vol.44: 1–5. ISSN 0067-1975

A New Species of *Sphenocarcinus* A. Milne Edwards, 1875 from Tasmantid Guyots, *S. lowryi* n.sp. (Crustacea: Decapoda: Brachyura) with Notes on the Taxonomic Status of the Genus

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ABSTRACT. A new species of *Sphenocarcinus* with a bifid rostrum, *S. lowryi*, is described from the Tasman Sea. This brings to 17 the number of species of the genus *Sphenocarcinus*.

RÉSUMÉ. Une nouvelle espèce de *Sphenocarcinus* à rostre bifide, *S. lowryi*, est décrite de la mer de Tasman. Cela porte à 17 le nombre des espèces du genre *Sphenocarcinus*.

RICHER de FORGES, B., 1992. A new species of *Sphenocarcinus* A. Milne Edwards, 1875 from tasmantid guyots, *S. lowryi*, n.sp. (Crustacea: Decapoda: Brachyura) with notes on the taxonomic status of the genus. Records of the Australian Museum 44(1): 1–5.

In May 1989, an expedition organised by the Australian Museum, Sydney on board the RV *Franklin* explored the Tasman Sea (Lowry, 1989). One aim of this expedition was the sampling of the benthic fauna living on the summit of the guyots. In the Tasman Sea, these guyots form several alignments parallel from north to south between 21°and 38°S (Kroenke *et al.*, 1983). These reliefs are the signs of a volcanic activity linked to a "Hot-spot" and to the movement south-north of the Indian-Australian plate (Slater & Goodwin, 1973; Rigolot, 1988).

The summits of these structures are relatively flat and can be worked by dredges and trawls; they reach heights between 90 and 900 m in depth, forming small islands of bathyal fauna, isolated from each other by abyssal depths (Fig.1).

Despite the difficulties encountered in working these hard bottoms with gears which were too fragile, 21 species of crabs belonging to 11 families were collected. From this collection, a series of specimens of the genus *Sphenocarcinus* A. Milne Edwards, 1875 are described as a new species.

This genus currently contains 16 species: four have a single rostrum composed of two spines of varying lengths and shapes. It has been recently been enriched by three new species, originating in New Caledonia (*S. orbiculatus, S. stuckiae*) and in the Philippines (*S. bipartitus*), described by Guinot & Richer de Forges

(1986a). Shortly afterwards, another new species was described from the north of New Caledonia: *S. mammatus* Guinot & Richer de Forges, 1986b.

Sphenocarcinus lowryi n.sp.

Fig.2A-C

Type material. HOLOTYPE: male, 14.6 x 13.8 mm (length without rostrum), Pacific Ocean, east coast of Australia, western Tasman Sea, Britannia Seamount, 28°17.04'S 155°36.46'E, 425 m, RV *Franklin*, 05-89, stn 46, 10 May 1989, coll. J.K. Lowry *et al.* (AM P39430).

PARATYPES: male 13.6 x 12.2 mm, female 9.7 x 8.3 mm, 9 juveniles 3.7 to 5.6 mm length, RV *Franklin*, 05-89, stn 46.

Ovigerous female 14 x 12.5 mm, female 8.6 x 7.5 mm, 2 juveniles 5.5 x 4.6 mm, 5 x 4 mm, RV *Franklin*, 05-89, stn 47, 10 May 1989, Britannia Seamount, western Tasman Sea, 28°17.47'S 158°37.89'E, 419 m, coll. J.K. Lowry *et al.* (AM P39431).

Etymology. This species is dedicated to Dr J.K. Lowry who directed the expedition.

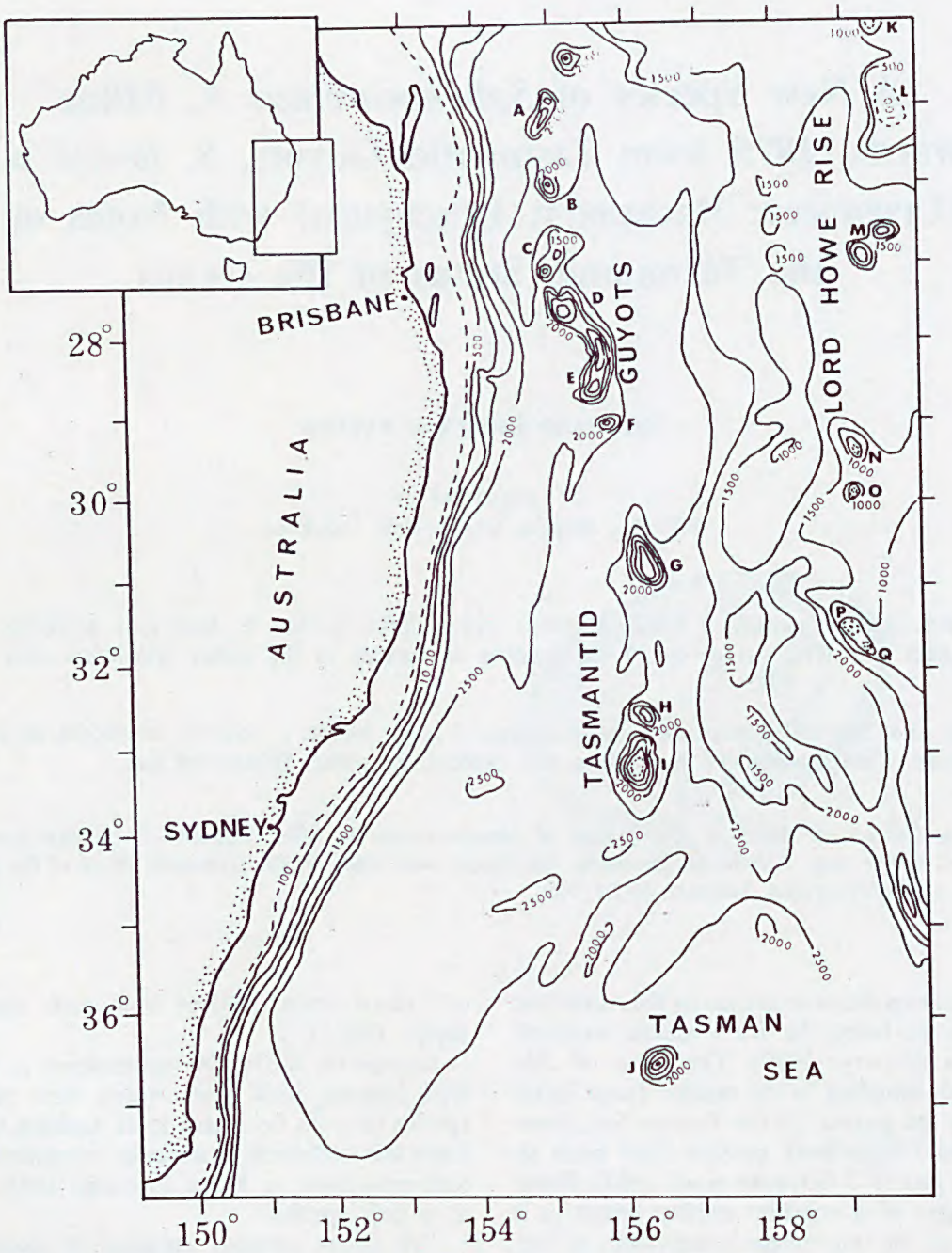

Fig.1. Bathymetric map of the Tasman Sea showing the alignments of guyots (from Slater & Goodwin, 1973). A: Recorder guyot: B: Moreton seamount; C: Brisbane guyot; D: Queensland guyot; E: Britannia guyots; F: Stradbroke seamount; G: Derwent Hunter guyot; H: Barcoo guyot; I: Taupo guyot; J: Gascoyne guyot; K: Kelso guyot; L: Capel guyot; M: Gifford guyot; N: Middleton Reef; O: Elizabeth Reef; P: Lord Howe Island; Q: Balls Pyramid.

Description. Pyriform carapace. Rostrum formed of 2 long divergent spines (left spine broken on holotype). Dorsal face bearing raised plates in relation to surface of carapace. A short but dense pubescence covers the carapace, including plates.

Dorsal plates disposed as follows: 1 uneven gastric plate, subcircular, whose lower edge rises to form a point; in front of and surrounding this plate, 3 tubercules; 1 circular plate, bearing, in the middle, a tubercle giving it the appearance of a cap, this plate being flanked laterally by 2 tubercules; on each side, a pair of branchial plates, the posterior pair pointing to the outside like a spine and the anterior pair set obliquely; these 2 branchial plates offer a concave surface in the shape of a saddle; a large L-shaped hepatic plate whose lower part serves as an edge for the orbit, with the posterior part ending in a spine which points towards the top of the carapace (it is in fact the point of the hepatic and postorbitary plates); 1 lengthened sub-hepatic plate, touching the edge of the buccal margin; back edge of the carapace widening in its middle section to form a spine facing posteriorly.

At the base of the 2 big rostral spines, 2 strong supraocular spines facing towards the outside. Short ocular peduncles. Wide basal antennal article and joined to the base of the rostrum. Smooth sternal plastron.

Individual variations. In the female, the pubescence is more marked, with long hooked setae here and there on the gastric plate and with long setae on the sides of the branchial areas.

In the juvenile, the plates are not as clearly differentiated, and are more like spines, especially the branchial and hepatic spines which are sharper than those of the adult. In a series, increasing in size from a juvenile (3.7 mm in length) to the an adult (14.6 mm in length), the transformation of spines into calcified plates can be observed.

Remarks. In the genus *Sphenocarcinus, S. lowryi* n.sp. is part of a group of species which has very developed plates, and, in particular, branchial plates which point laterally. In this group, the closest species are: *S. velutinus* Miers, 1886, *S. luzonicus* Rathbun, 1916, *S. coralliophilus* Takeda, 1980, *S. bipartitus* and *S. stuckiae* Guinot & Richer de Forges, 1986a.

Sphenocarcinus lowryi n.sp. is easily distinguished from *S. velutinus* by the absence of raised nodules forming plates characteristic of the latter. *Sphenocarcinus luzonicus* has plates which are rounder and smoother than those of *S. lowryi* n.sp., and the hepatic plate does not form a spine as does that of *S. lowryi*. Furthermore, with *S. luzonicus* all the plates show a convex bulge, while the branchial and hepatic plates have a concave curve in *S. lowryi* n.sp.

The species described by Takeda (1980) from Midway Island under the name of *S. coralliophilus* has branchial plates which are very sharp and which point laterally,

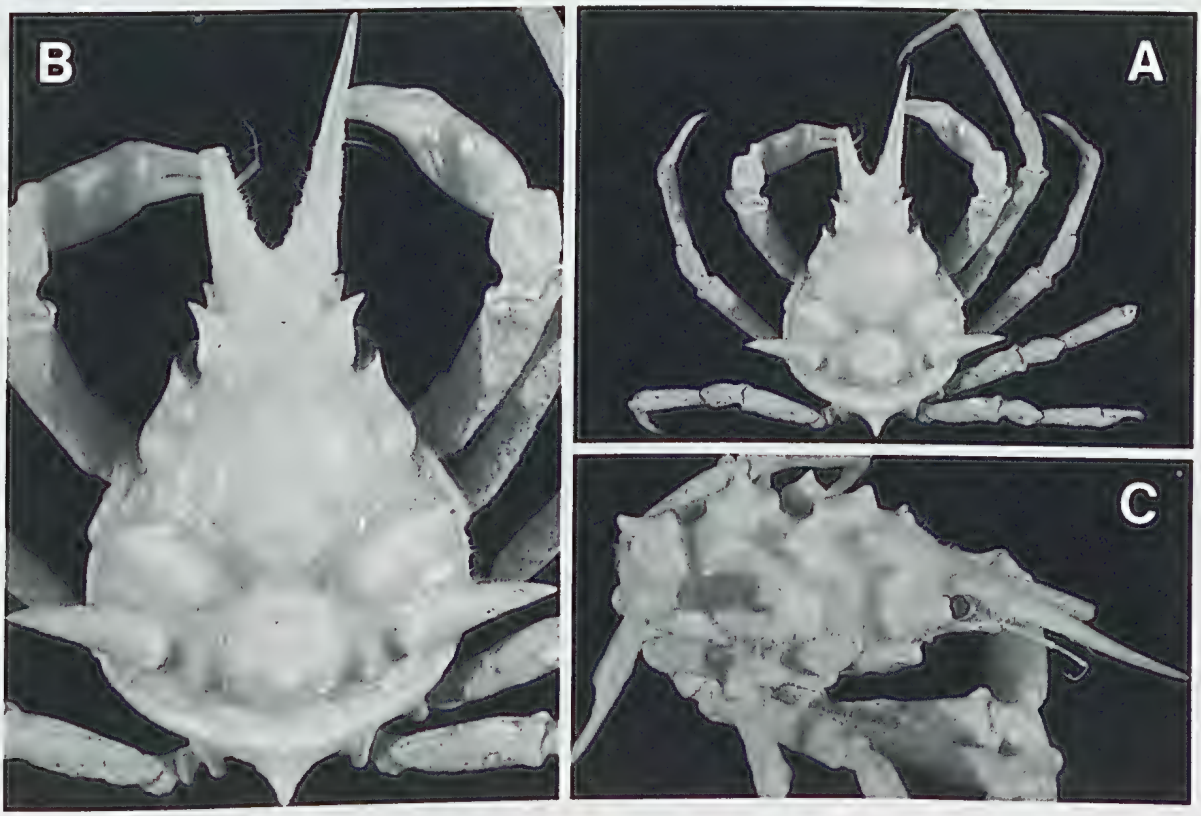

Fig.2. *Sphenocarcinus lowryi* n.sp., holotype, male, 14.6 x 13.8 mm, east coast of Australia, Tasman seamount, 28°17.04'S 155°36.46'E, 425 m, RV *Franklin*, 05-89, Stn 46, 10 May 1989, coll J.K. Lowry *et al.* (AM P39430). A: full view; B: close-up of carapace; C: profile.

comparable with those observed in *S. lowryi* n.sp. However, it is distinguished from it by the absence of a supraocular spine and by the present of very sharp hepatic spines pointing laterally, while those of *S. lowryi* n.sp. are not at all sharp and point upwards. Finally, *S. coralliophilus* carries a posterior plate, below the cardiac plate, which is absent in *S. lowryi* n.sp.

Sphenocarcinus lowryi n.sp. exhibits a certain resemblance to *S. stuckiae*, described from New Caledonia, by the presence of a posterior edge of the carapace forming a spine and by its long rostral spines. *Sphenocarcinus lowryi* is easily distinguished by the presence of supraocular spines, which are absent in *S. stuckiae*.

Sphenocarcinus bipartitus, described from the Philippines, has pointed branchial plates which are slightly concave, similar to those of *S. lowryi* n.sp., and also has supraocular spines. This species is distinguished from *S. lowryi* n.sp. by the reduction of cardiac and gastric plates, which are replaced by protuberances bearing setae. To sum up, *Sphenocarcinus lowryi* n.sp. can be distinguished from all other species by the simultaneous presence of concave spines, a cardiac plate topped by a cap, supraocular spines, and a posterior spine.

Using the diagnoses proposed by Garth (1958) and Griffin & Tranter (1986) the genus *Sphenocarcinus* A. Milne Edwards, 1875, is considered synonymous with *Rochinia* A. Milne Edwards, 1875. After the description of *S. mammatus*, Guinot & Richer de Forges (1986) checked the species attributed to this genus, and had noted its difficult separation from the genus *Rochinia*.

Although these considerations go beyond the aim of this article, it seems nevertheless that the genus *Sphenocarcinus* is justified by a single character: the presence of calcified plates on the carapace. It is true that the 'frontier' with the genus *Rochinia* is often poorly defined: for example, *S. nodosus* Rathbun, 1916, which has no plates, seems distant from other species of this genus.

I note that with *S. lowryi* n.sp. the calcified plates are former spines modified during the growth period. I have not observed this phenomenon in *S. orbiculatus*, for which an abundant amount of material, including juveniles, has been examined.

Arguments which use the male pleopod to separate the genera do not seem adequate, and the criterion of sexual appendices is generally little used with the Majidae.

In the *Sphenocarcinus* group of the Indo-Pacific species, as it is currently understood, three types of rostrum can be distinguished: a bifid rostrum but with parallel jointed spines (*S. auritus*); an uneven rostrum, but bifid at the end (*S. cuneus, S. aurorae, S. difficilis, S. pinocchio*), these species all having strong calcified plates; a clearly bifid rostrum starting from the base with divergent spines. In this group (*S. stimpsoni, S. velutinus, S. bipartitus, S. stuckiae, S. mammatus, S. orbiculatus, S. nodosus, S. luzonicus, S. sphenocarcinoides, S. carbunculus, S. bidens, S. coralliophilus* and *S. lowryi*) two species possess carapace plates different from that of the others: *S. velutinus* and *S. nodosus*.

Sphenocarcinus velutinus (Miers, 1886) has a carapace covered with a strong pubescence masking the outline, the nodosities are rounded and do not form plates except in the branchial zone. The only rough patches really comparable to the plates of the other species are the two flat plates on the lateroventral edge. This species, originally placed in the genus *Pugettia*, was moved to *Sphenocarcinus* by Griffin (1976) after examining unstudied specimens from the *Albatross*. This material was later described as a new species, *S. bipartitus* Guinot & Richer de Forges, 1986. Sakai, 1976, suggested placing this species in the genus *Rochinia*.

Sphenocarcinus nodosus Rathbun, 1916, whose holotype we have studied, has on the cephalothorax, rounded nodosities covered with a tomentum but not true plates, the rostral spines are very short and the carapace is rounded. The combination of these characters states isolates it from the genus *Sphenocarcinus*.

In conclusion, it appears that the genus *Sphenocarcinus* is heterogenous and that it should be divided into two or three taxonomic categories. However, it contains a group of species which, regardless of their size, show strong calcified plates on the dorsal face. It is this group which constitutes the true *Sphenocarcinus, sensu stricto* distinct from *Rochinia*.

Distribution. *Sphenocarcinus lowryi* was collected on the tops of submarine mountains in the Tasman Sea, off the east coast of Australia, on hard bottoms, at depths of 419 to 425 m.

Although very close to the Chesterfield Islands (2100 km), and to New Caledonia (2700 km), the Britannia guyot seems to possess a particular benthic fauna.

ACKNOWLEDGMENTS. I wish to thank the scientific team which took part in the exploration of the Tasman Sea, and more specially the expedition leader, J.K. Lowry, who entrusted me with material for research. Dr D. Guinot has kindly checked the manuscript and has shared with me her experience of the Majidae.

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Addendum

When this paper was in press, Tavares (1991) proposed a new classification of this group. He limited the genus *Sphenocarcinus* for the two American species, placed the *Sphenocarcinus* with bifid rostrum and short chelipeds under *Rochinia* and those with long chelipeds under *Oxypleurodon,* and created a new genus *Nasutocarcinus* for the single rostrum species.

In the Tavares view, our *S. lowryi* n.sp. would be placed under *Rochinia.*

TAVARES, M.S., 1991. Redéfinition des genres *Rochinia* A. Milne Edwards, *Sphenocarcinus* A. Milne Edwards et *Oxypleurodon* Miers, et établissement du genre *Nasutocarcinus* gen. nov. (Crustacea, Brachyura, Majidae). Bulletin du Muséum national d'Histoire naturelle, Paris. Sec. A(1-2), sér. 13(4): 159-179.

Revision of the Species Previously Associated with the Australian Scincid Lizard *Eulamprus tenuis*

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ABSTRACT. *Eulamprus tenuis*, a moderate-sized, robust-limbed skink from the east coast of Australia, is shown to be a composite of five species, only three of which have available names. All five species are reviewed taxonomically and a resumé of their general natural history is provided.

GREER, A.E., 1992. Revision of the species previously associated with the Australian scincid lizard *Eulamprus tenuis*. Records of the Australian Museum 44(1): 7–19.

This is a review of the alpha taxonomy of the species either currently or recently confused with *Eulamprus tenuis*, a saxicolous/arboreal, shade-loving to crepuscular scincid lizard of the woodlands and forests of the east coast of Australia. The most recent review of the Australian herpetofauna recognises only one species with two subspecies (Cogger, 1986). However, there are five species, only three of which have names. This paper reviews this complex of species and describes the unnamed species.

Definitions and Abbreviations

Two scales systems require special definition for the purposes of this paper. Nuchal scales are all those transversely enlarged paravertebral scales behind the parietal scale which either touch the parietal or touch another enlarged paravertebral; the nuchal scale count is the total number of nuchal scales on both sides.

Subdigital lamellae are all those scales on the ventral surface of the fourth toe of the pes counted between the claw and the level of the bifurcation of the third and fourth digits.

Abbreviations used are: AM – Australian Museum; MNHP – Museum National d'Histoire Naturelle, Paris; NP – National Park; NHRM – Naturhistorika Riksmuseet, Stockholm; NS – not significant statistically at the .05 level; QM – Queensland Museum; QNPWS – Queensland National parks and Wildlife Service; SF – State Forest.

One, two or three asterisks indicates probability levels of .05, .01 and .001, respectively.

Table 1 is contained in the Appendix.

The Phylogenetic Relationships of the *Eulamprus tenuis* Complex

There is no particular reason to think that the species previously confused under the name *Eulamprus tenuis* are the closest living relatives of each other, apart from their general similarity. They show only three clearly

derived character states *vis à vis* the other members of their major lygosomine group, the *Sphenomorphus* group, and all characters – reduced auricular lobules, medially expanded palatal rami of the pterygoids, and ovoviviparity – occur in many other members of the *Sphenomorphus* group. In fact, the lack of derived characters may be telling us something equally interesting, i.e., that they are very generalised members of the *Sphenomorphus* group and hence perhaps not too dissimilar to the ancestor of this group. In this regard there are two additional features of their biology that are possibly also retained primitive behavioural characters: their relatively conspicuous arboreal/saxicolous habits and their at least partial diurnality. These habits contrast with the cryptozoic, semifossorial and crepuscular to nocturnal habits of many members of the *Sphenomorphus* group.

Recognising the *Eulamprus tenuis* complex as an assemblage of relatively primitive *Sphenomorphus* group species leaves unanswered the question of how to diagnose the contained species. The easy way might be to refer to a regional fauna (e.g., Cogger, 1986) for a 'diagnosis' of *E. tenuis*, at least amongst the Australian representatives of the *Sphenomorphus* group, and then diagnose the five species against each other. However, this would beg the question of a diagnosis against the rest of the group as a whole. Therefore, in order to put the species diagnoses on a more rigorous footing, a list of characters follows that will distinguish the *E. tenuis* complex from all other species in the group worldwide and then diagnose the species in the complex against each other. The characters that distinguish the complex are as follows (derived characters are marked by a solid diamond symbol): head scales generally unfragmented; supraoculars four, first two on each side contacted by frontal; frontoparietals distinct; lower eyelid scaly, moveable; tertiary temporals contacting lower secondary temporal two; external ear opening relatively large, with only low auricular lobules anteriorly◆; postmental contacts first two infralabials on each side.

Size moderate (max. SVLs range 66-86 mm); limbs well developed, pentadactyl; body scales smooth, cycloid; subdigital lamellae smoothly rounded; supradigital scales in multiple rows except for last three scales which are single.

Presacral vertebrae 26; cervical vertebrae eight; phalanges in manus/pes: 2.3.4.5.3/2.3.4.5.4.

Postorbital bone present; parietal foramen present; premaxillary teeth 7-9; palatal rami of pterygoids medially expanded◆, and entering infraorbital vacuity.

Inguinal fat bodies present.

Peritoneum of body cavity dark.

Ovoviviparous◆.

Implicit in this extended taxonomic treatment of the *Eulamprus tenuis* complex is a belief that the genus *Eulamprus* is not a particularly stable taxonomic concept. The original concept of the genus included only *E. quoyii* and was proposed without a diagnosis (Fitzinger, 1843). A subsequent concept included all the 'water skinks' – *E. heatwolei*, *E. kosciuskoi*, *E. leuraensis*, *E. quoyii*, and *E. tympanum*, a group which while probably monophyletic (Shea & Peterson, 1985; Wells & Wellington, 1985; Greer, 1990) was not diagnosed when proposed (Wells & Wellington, 1984).

The current concept of *Eulamprus* includes the water skinks, the *E. tenuis* complex and *E. amplus*, *E. luteilateralis* and *E. murrayi* (Cogger, 1986; Greer, 1990) but has as its sole derived character ovoviviparity, a character which is not unique in the *Sphenomorphus* group. It would not be too surprising, therefore, if future work showed that *Eulamprus*, as now conceived, is polyphyletic.

Key to the Species of the *Eulamprus tenuis* Complex

1. Upper secondary temporal overlaps lower 2

—— Upper secondary temporal overlapped by lower 4

2. Enlarged nuchals (total both sides) 2-10, mode 4-6; subdigital lamellae 17-23; nuchal area without dark midline streak; vomers distinct 3

—— Nuchals (total) 0-4, mode 2; subdigital lamellae 22-27; nuchal area often patterned with dark midline streak; vomers fused ..... *E. tenuis*

3. Midbody scale rows 28-32; ground colour medium brown, dorsal pattern dark brown; wetter areas ..... *E. brachysoma*

—— Midbody scale rows 32-38; ground colour light brown, dorsal pattern medium brown; drier areas ..... *E. sokosoma*

4. Paravertebral scales 55-64; nuchal area without dark midline streak ..... *E. martini*

—— Paravertebral scales 69-74; nuchal area with dark midline streak ..... *E. frerei*

Eulamprus brachysoma (Lönnberg & Andersson)

Fig.1

Lygosoma brachysoma Lonnberg & Andersson, 1915: 5 (type locality - Atherton, Qld; holotype - NHRM 3211).

Material examined. All locations are in Queensland. AM 4722, R 5709, 47135-37 - Gayndah; R 2195-16 - Brisbane; R 9942, 9944, 11169-72, 47100-47103 - Lindeman Island; R 11097, 11720, 11724, 11726, 47229 - Hayman Island; R 13534- 35, 19717 - Brampton Island, 32.2 km north-east of Mackay; R 16541 - Coen; R 17045 - Saint Ronans; R 21322 - 53.1 km south of Laura; R 26703 - Endeavour River, 14.5 km west, 3.2 km north of Cooktown; R 26829-30 - Big Tableland, 27.4 km south, 3.2 km east of Cooktown; R 38046-47 - Proserpine; R 45798-99, 49860 - Holbourne Island, near Bowen; R 45806 - Cairns; R 47224 - 2 km west of Ravenshoe; R 47225 - Trinity Bay between Hartleys Creek and Port Douglas; R 47226 - 3.2 km west of Snubby Creek, Millstream Falls District, Ravenshoe; R 47227-28 - Brumby Gully between Kuranda and Emerald Creek; R 49862 - Pine Islet; R 49863-64 - Edward Island; R 57773 - 24.2 km south of Stuart Creek south of Townsville; R 58933 - Ravenshoe; R 61598-600 - Arcadia Valley via Injune; R 62486 - forestry camp, Windsor Tableland; R 62744 - Dent Island; R 62745, 62747 - Eshelby Island; R 63017-24 - 11.9 km south-south-east of Springsure Post Office; R 63134 - 2.9 km north-north-east of the Gulf Highway via Kennedy Highway (40 Mile Scrub); R 86319 - approximately 10.9 km west of Mareeka Post Office by road; R 86320-21 - 16.4 km south-east of the Bruce Highway via Gilles Way, near Gordonvale; R 111595-96, 111604-05 - Crystal Cascades; R 111603, 111618-19 - Granite Gorge; R 111607 - Cape Cleveland; R 114039 - just south of Finch Hatton NP; R 120576, 122959 - Cape Hillsborough.

QM J 1730, 1802-07, 1810-20, 1822-1825, 1826-1830 - North Queensland; 1732-36 - Cape York?; J 1831-1833 - Cardwell; J 3885, 5638 - Lindemann Island; J 3889, 3891-92 - Holbourne Island; J 10365 - Proserpine; J 11150 - Shiptons Flat; 49 km south of Cooktown; J 12130 - Tinaroo Dam, Atherton Tableland; J 15627 - Pine Mountain, Marlborough Station, north of Marlborough; J 15667 - Yebna Station, 80 km east of Injune; J 15741 - Coominglah SF, near Monto; J 17835-36 - Shipton's Flat, 32.2-48.3 km south of Cooktown; J 19336-37 - Mount Molloy; J 20510, 20564 - Melville Range, Cape Melville; J 22665 - Big Tableland, approximately 32.2 km south-east of Cooktown; J 23536 - Curraghmore, Mitchell River Crossing; J 24525 - Watsonville; J 24953-54 - Burnett River, Goodnight Scrub; J 25210 - Home Rule Falls, south of Cooktown; J 25319 - Amos Bay; J 25565 - 15 km from Gordonvale, along Gillies Highway; J 25909-25914 - Arcadia Valley via Injune; J 26111 - Hinchinbrook Island; J 27087 - Mount Cook; J 27119 - Roberts Turnoff; J 28488-90 - Blackdown Tableland, Mimosa Creek; 31020, 31023, 31052 - 40 Mile Scrub, 64.4 km west of Mount Garnet; 32786, 32788 - site 13, Brandy Creek; 32787 - creek adjoining site 13, Brandy Creek; 33865, 33878, 33895-99, 33964 - Oaky Creek, adjoining site 10, Homevale; 33868, 33888, 33947 - site 10A, Homevale; 33972, 33974, 33976 - Hill 609, Homevale; 33989-33991 campsite, Finch Hatton NP; 34033 - site 9, Finch Hatton NP; 34065 - adjoining site 9, Finch Hatton NP; J 34094 - site 9A, Finch Hatton NP; J 36802 - Glenorina; J 36803 - Dunlow; 36804 - Emerald; J 37295 - Mount Coot-tha; J 38511 - Robinson Gorge area, Glenhaughton; J 38512 - Tommy Creek, Glenhaughton; J 38616-17 - Glenhaughton Creek, Robinson Gorge Road; J 38618-20 - Nathan Gorge; J 39166 - Byanda Station, 20 km north-north-west of Proston; J 39432 - Crystal Cascades, 12.5 km west of Cairns; J 39873-75 - Bakers Blue Mountain, 17 km west of Mount Molloy (900 m); J 40635 - Windsor Tableland, 26

Fig.1. *Eulamprus brachysoma* (AM R 61598) from Arcadia Valley via Injune, Qld.

km north-north-west of Mount Carbine; J 41324-25 - Crystal Creek, Mount Spec; J 41974 - South Percy Island, Percy Isles; J 41982 - Table Mountain, 20 km south-west of Rockhampton; J 42083 - 7 km west of Chillagoe; J 42160 - Kroombit Tops; J 42410-11 - approximately 15 km east of Gayndah on Gayndah - Ban Ban Springs Road; J 42508 - Jourama Falls NP; J 42509 - Mount Spec NP; J 42510 - Mount Spec, Townsville; J 42511-12 - Little Crystal Creek, Mount Spec NP, Townsville; J 42514-15 - Blue Water Range, north of Townsville; J 42518 - Hervey Range, west of Townsville; J 42527 - locality unknown; J 44037 - Mareeba; J 44299 - Warang, White Mountains; J 44578 - "Glencoe"; J 44596 - "Cardigan"; J 44687-88 - "Spyglass"; J 44838 - "Powlathanga"; J 45388 - summit of Mount Mulligan; J 45565 - Granite Gorge via Mareeba; J 46297-301 - Carlisle Island; J 46747 - Fairybower Road, approximately 8 km west of Rockhampton.

QNPWS: RS 110 - Millstream Falls NP; R 174 - Lindeman Island; R 306 - Jamie Creek, Walsh River; R 576 - Brampton Island NP; R 633, 11004 - Cape Hillsborough NP; R 635, 751 - Eungella NP; N 11308 - Newry Island NP (near Seaforth); N 11877, 11900 - Cape Hillsborough NP; N 11921 - Smalleys Beach, Cape Hillsborough NP; N 11953-54; Long Island NP; N 12005 - Redbill Island; N 12078 - South Molle Island; N 17798 - Levers Plateau, near Lamington NP; N 25686 - Yarra-mulla Station; N 25829 - no data; N 36561, 36564 - Broadwater Creek NP boundary; N 54764 - Bathurst Head, near Princess Charlotte Bay; N 58406; Conway Headquarters, Conway NP; N 58450.

Diagnosis. Differs from other members of the *Eulamprus tenuis* complex in the following combination of characters: upper secondary temporal overlaps lower; transversely enlarged nuchal scales 2-10, mode 6; subdigital lamellae fourth toe 17-23; nuchal area without dark midline streak; midbody scale rows 28-32.

Distribution. On the mainland, from Coen on Cape York Peninsula south to Gayndah and possibly Brisbane (if the locality is correct for AM R 2915-16); occurring inland as far as just south-south-east of Springsure and offshore on continental islands from Hinchinbrook Island south to the Percy Isles (Fig.2).

The Coen record (AM R 16541) has been questioned on the grounds that subsequent extensive faunal surveys in the area have failed to reveal additional specimens (K. McDonald, *in litt.*). However, there is no basis to fault the data associated with the specimen.

Habitat. Moist woodland to closed shrubland and forest.

Habits. Arboreal and saxicolous; sometimes on man-made structures (e.g., cinder block structures); diurnal in shade (all observations based on K. McDonald personal communication and personal observation).

Reproduction. Ovoviviparous. Twenty four ovigerous or gravid females were found amongst the specimens examined. These ranged 52-74 mm SVL (mean = 64.6). For the 20 gravid females for which follicle number or litter size could be determined, there was a positive correlation between female size and follicle number/litter size (r = .58**); female size for these 20 specimens ranged 52-74 mm (mean = 64.9; sd = 6.12) and follicle number/litter size 2-5 (mean = 3.8; sd = 0.95).

Of the 13 gravid females with collection dates, those with enlarging follicles were collected in the period 6 June to 12 July (N = 4) and 18 April (N = 1), and those with oviducal young in the period 29 September to 12 December (N = 8). Relating these data to the seasons of north-eastern Queensland (the southernmost gravid female is from the vicinity of Springsure) suggests that

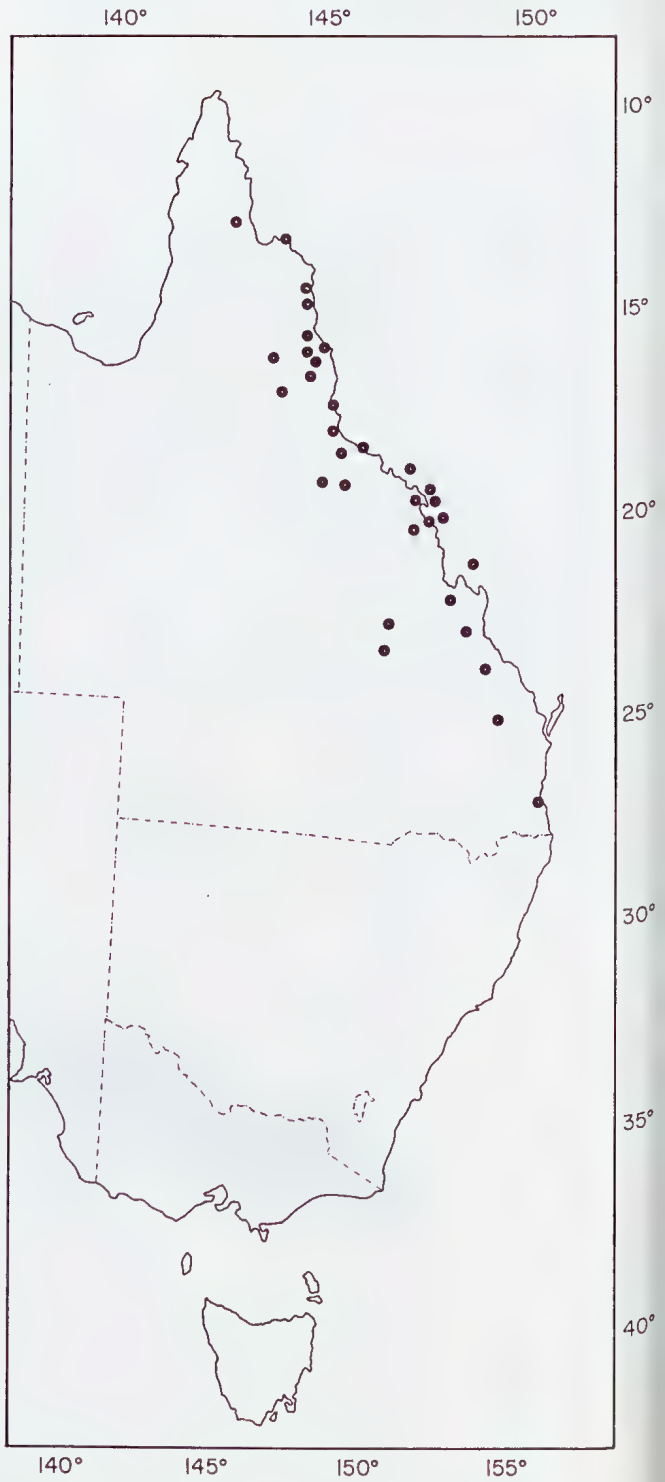

Fig.2. The distribution of *Eulamprus brachysoma.*

females carry yolking follicles in the late wet season to the late dry season and oviducal young in the late dry season to the early wet season. Birth probably occurs in the middle of the wet season.

Comparison with similar species. *Eulamprus brachysoma* is most similar to *E. sokosoma*, a species which occurs almost entirely within its general range. The surest way to tell the two species apart is on the midbody scale row count – *Eulamprus brachysoma* has 28-32 scale rows whereas *E. sokosoma* has 32-38 (only 4% of specimens have as few as 32). In addition *E. brachysoma* is generally darker and slightly more gracile whereas *E. sokosoma* is lighter and more robust, especially in the body. Ecologically, *E. brachysoma* appears to occur in slightly more mesic habitats while *E. sokosoma* occurs in slightly more xeric habitats.

Comment. I have been unsuccessful in borrowing the holotype of *Eulamprus brachysoma* (Lönnberg & Andersson, 1915; NHRM 3211), but I have been able to examine two photographs of the specimen taken by H.G. Cogger. There is no doubt that this specimen is a member of the widespread northern Queensland population delineated here.

Eulamprus martini (Wells & Wellington)

Figs 3,4

Concinnia martini Wells & Wellington, 1985: 26 (type locality - Yabbra State Forest, 3.9 km south of Urbenville, NSW; holotype - AM R 116966).

Material examined. AM R 4050 - Nerang River, Qld; R 5029 - Nambor, Qld; R 8567 - Tweed River, NSW; R 8940 - Mount Tambourine, Qld; R 13120 - Tenterfield, NSW; R 16470, 16665 Yepoon, Qld; R 26128 - Biloela, Qld; R 26144 - Grafton District, NSW; R 29619 - Wintervale Road, 6.4 km north of Dalmorton, NSW; R 29656 - Mount Norman, Wallangarra, Qld; R 30366 - Windohra, Qld; R 47105 - 78.9 km east of Glen Innes on Grafton Road, NSW; R 47106-07 - Obon River, 43.5 km north-east of Guyra, NSW; R 47108 - 8.1 km south-east of Bolivia, NSW; R 47109-11 - 11.3 km north of Deepwater on New England Highway, NSW; R 47112-17 - 11.3 km west-south-west of Tenterfield, NSW; R 47118-30 - 4.8 km south-west of Tenterfield, NSW; R 47131-32, 47134 - 20.9 km south of Tenterfield, 14.5 km from Sandy Flat on Mount Speribo, NSW; R 47184-85, 47187-88 Coffs Harbour, NSW; R 47186 - Glenreigh, NSW; R 54725 - Kumbaingeri Sanctuary, Coffs Harbour; R 54851 - Merbin SF, Murwillumbah area, NSW; R 57772 - Tooloom Falls, NSW; R 58432-33 - Bungulla, NSW; R 58434 - Queen Marys Falls near Killarney, Qld; R 58435-39 - Wilsons Peak, Qld; R 58440 - 8.1 km from Landsborough on Nambour Road, Qld; R 58441-44 - Yandina, Qld; R 58445 - 16.1 km from Mount Tambour, Qld; R 58446 - Tambourine Mountain, Qld; R 58447 - 12.9 km from Canungra on Nerang Road, Qld; R 58448 - 8.1 km south of Grafton, NSW; R 58460 - 18.5 km from Nymboida on Tyringham Road, NSW; R 58461 - Tooloom Falls, NSW; R 58468 - 6.4 km north of Glenreagh, NSW; R 58469 - Glens Creek, 38.6 km west of Grafton, NSW; R 58470-71 - Tooloom

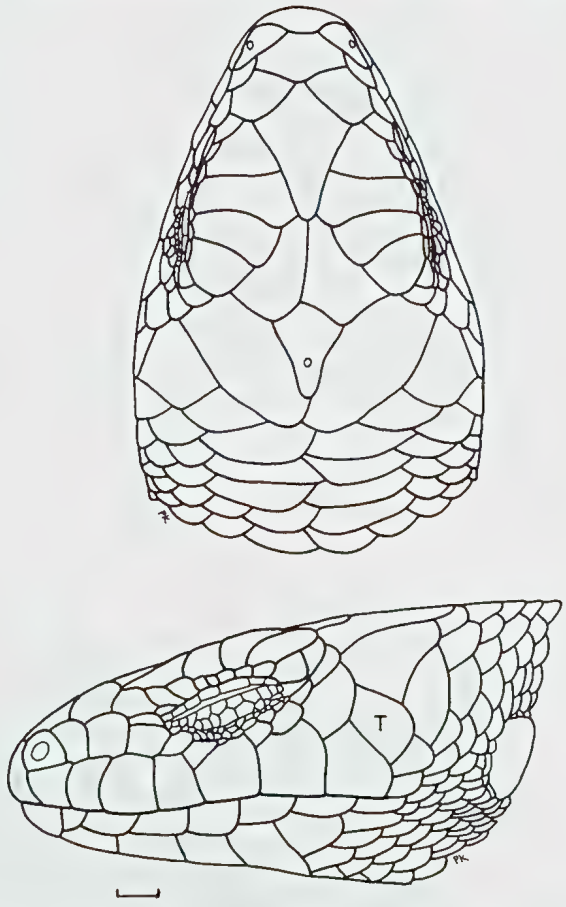

Fig.3. *Eulamprus martini* (AM R 86292). Note how the lower secondary temporal (T) overlaps the upper; compare Figures 7 and 11. Bar scale = 1 mm.

Fig.4. *Eulamprus martini* from Girard SF, north-north-west of Drake, NSW.

Falls, NSW; R 58472 - Battens Bight Creek, 41.8 km south of Casino, NSW; R 61597 - Conondale Range, Qld; R 61602 - Maleny, Qld; R 61603 - Boonoo Boonoo, NSW; R 61604 - Helidon, Qld; R 61605 - Jimna area, Qld; R 74027 - 18.5 km from Nymboida on Tyringham Road, NSW, R 86288-96 17.5 km south-west of Bolivia Post Office via New England Highway, NSW; R 86297-98 - Loop Lookout just north of Cougal, NSW; R 86299; 8.1 km west of Drake Post Office via Bruxner Highway, NSW; R 86300 - 30.0 km south of Whiporie by Road, NSW; R 86301-03 - Bowenia forestry office, Bowenia, Qld; R 92300 - 14 km north of Coffs Harbour

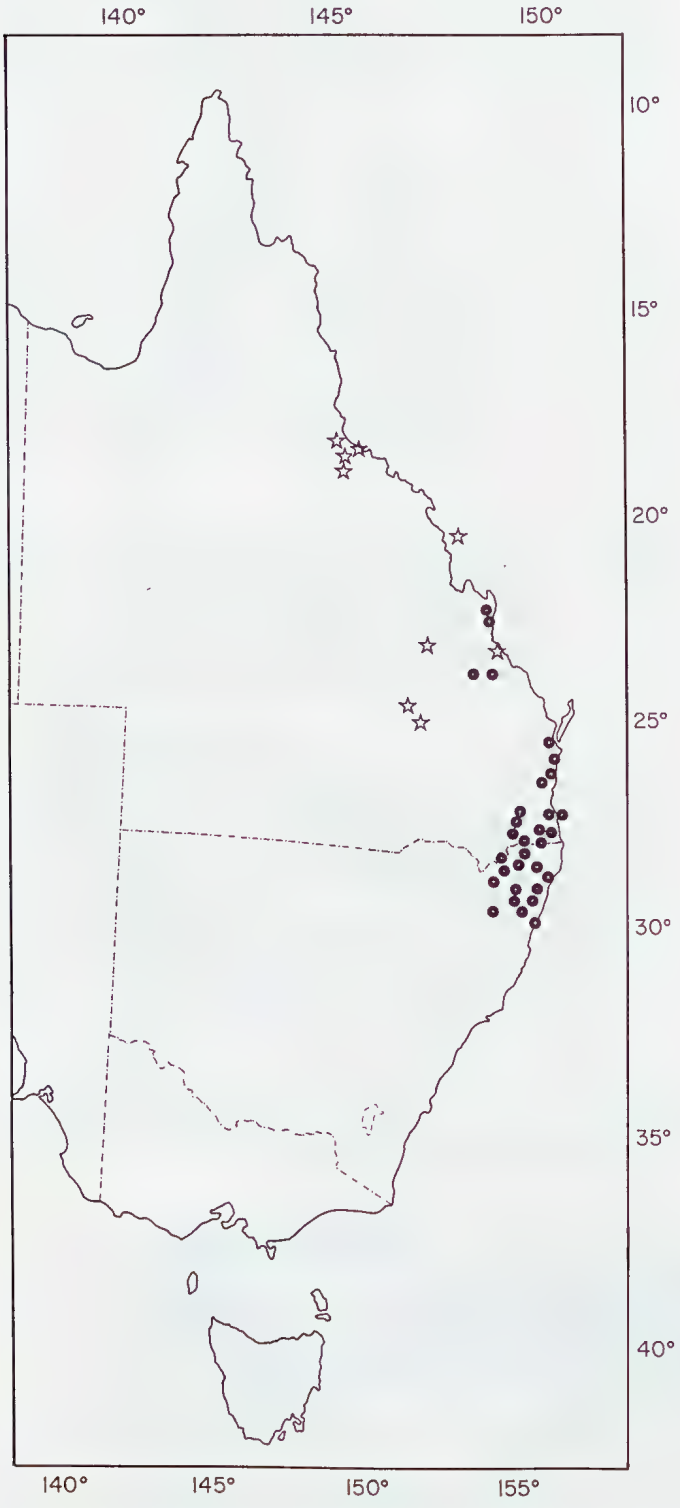

Fig.5. The distribution of *Eulamprus martini* (closed circles) and *E. sokosoma* (stars).

on Pacific Highway, NSW; R 96432 - 1 km west of Amiens, Qld; R 96438, 97167 - Wilsons Downfall, NSW; R 96833 - 250 m north of Lookout, Washpool Granite Preserve, NSW; R 96842-45 - Lookout area, Washpool Granite Preserve, NSW; R 96862, 96884, 96931 - 2.5 km north of Tin Ore Creek, north-west fire trail, Gibraltar Range NP, NSW; R 112291-92 - Bom Bom SF, NSW; R 113127 - Dyraaba Creek, 23 km west of Casino on road to Tenterfield, NSW; R 113359 - 1.0 km from Frenchville Road via Pilbeam Drive, base of Mount Archer, Rockhampton, Qld; R 114072-73 - approximately 22 km south-east of Tenterfield via Billyrimba Road, NSW; R 115531 - 20.0 km north-west Yangan, Qld; 116966 - Yabbra SF, 3.9 km south of Urbenville, NSW (holotype of *S. martini*).

Queensland Museum (all localities in Queensland unless stated otherwise): J 1717-19, 1722-27, 1929 - Qld; J 1720 - Rockhampton; J 1809 - North Qld; J 1821 - North Qld; J 2420 - Brisbane district; J 2846 - Currumbin; J 2854 - Redbank Plains; J 4827, 17572 - Museum gardens, Brisbane; J 6578 - Annerley, Brisbane; J 7540 - Kangaroo Point, Brisbane; J 7924 - Qld Museum gardens; J 8107 - Eukey; J 8889-95 - Pyramid Creek, east of Wybera; J 10874 - Qld Museum, Brisbane; J 11044 - Acacia Ridge, Brisbane; J 11498 - Southport; J 12115 - 3 km north of Coulson; J 12116 - 7 km east of Coulson; J 12117 - Museum grounds, Brisbane; J 12118 - 6 km south of Ferndale; J 12120 - St Lucia, Brisbane; J 12121 - at top of Gwydir Highway, NSW; J 12122 - northern NSW; J 12127 - North Sydney, NSW; J 12128, 13926 - Wyberba; J 12129 - 5 km from Petrie, near Dohle's Rocks; J 12133, 12135-36 - Cedar Creek Falls, Mount Tamborine; J 12137 - 8 km east of Wyberba; J 13706 - Mount Roberts; J 13820 - NP; J 14140 - Mitchell River Mission, Magnificent Creek; J 14219-20 - Emu Vale; J 14248 - Swanfels; J 16792 - 1.6 km east of Tangalooma, Moreton Island; J 22181 - 10 km south-west of Point Lookout, N. Stradbroke Island; J 22312 - Mount Gravatt, Brisbane; J 22686 - Hamilton; J 23654 - Mount Cootha; J 23693 - Mount Glorious; J 24069 - Mount Nebo; J 25762 - The Lair, Limestone Ridge; J 29920 - Maleny; J 29939 - 3.2 km east of Lake Cookameera, Cooloola; J 30234 - near Missings Bridge, Tinana Creek; J 30544 - Upper Emu Creek at foot of Mount Superbus near Warwick; J 30771-72 - Jimna, Yabba Top Road; J 31523-25 - near Mount Flinders; J 31699 - Girraween NP; J 33969 - Hill 609, Homevale; J 34113 - Boonoo Boonoo Falls via Tenterfield, NSW; J 34963 - Turners Dip, near Picabeen, Tweed River Valley; J 35367 - 1.5 km south of "The Breadknife", Booloumba Creek, Conondale Ranges via Kenilworth; J 36932 - Conondale Range, Coonoon Gibber Creek; J 37181 - Rochdale SF; J 39301 - 36 km south of Gatton on Gatton - Warwick Road; J 39541-44 - Bauple SF via Gympie; J 39598 - Daisy Hill SF (R 215); J 40116, 40139 - Kroombit Tops (campsite 2nd causeway from logging huts on Ubobo Road); J 40135 - Kroombit Tops, approximately 1.5 km east of campsite); J 40136 - Kroombit Tops, northern escarpment, approximately 14 km north of logging huts; J 40357 - Girraween via Stanthorpe; J 41367 - Kelvin Grove; J 41553 - East Brisbane; J 42161, 47610 - Kroombit Tops; J 43955 - Upper Dry Creek, Kroombit Tops, 45 km south-south-west of Calliope; J 44287 - East Branch, Maranoa River near Warrang.

QNPWS (all localities in Queensland): RS 20 - Girraween NP; RS 59-60 Bauple SF; RS 80 - Harry Spring's Hut, Noosa River (near Lake Cootharaba); R 92 - Camp Milo, Cooloola SF; R 148 SF No. 958 Gundiah (part of Bauple SF); R 162 - Cunninghams Gap NP; R 192 - Burleigh Heads NP; R 250, 293 - Crows Nest NP; R 316 - Ravensbourne NP; R 370 -

Toolara SF; R 514, N 17110-11 - Girraween NP; N 17317 - Wilco Logging area, Bellthorpe SF; N 17320 - Sunday Creek SF; N 17666; Sandy Creek, Bellthorpe SF.

Diagnosis. Differs from all other members of the *Eulamprus tenuis* complex in the following combination of characters: upper secondary temporal overlapped by lower; paravertebral scales 55-64; nuchal area without dark midline streak.

Distribution. On the mainland from the Rockhampton–Yeppoon area in Queensland south to Coffs Harbour in New South Wales, inland as far as the Biloela area in Queensland and the area between Tenterfield and just north-east of Guyra in NSW; offshore known only from Moreton Island and North Stradbroke Island (Fig.5). The Sydney locality (QM J 12127) is assumed to be in error due to its grossly disjunct position.

Habitat. Vine thickets, open forest to woodland; also in clearings in these habitats. Probably only rarely, if ever, in closed forest. Occasionally on man-made structures (e.g., cement barbecue pits) and in houses (field notes associated with AM specimens; Czechura & Miles, 1983).

Habits. Arboreal and saxicolous, being found on logs and stumps and under exfoliating rock. Often out during the day.

Reproduction. Ovovipiparous. The 23 ovigerous and gravid females found in the collections examined ranged 50 to 71 mm SVL (mean = 62.3; *sd* = 4.52) and had follicle number/litter sizes ranging 2 - 6 (mean = 3.5; *sd* = 1.20). There was no significant correlation between female size and follicle number and litter size (r = .35 NS).

Fifteen of the females, all with oviducal young, have dates of collection. Fourteen of these females came from south of 26°S; they were collected between 20 October and 6 February. The one female from north of 26°S (vicinity of Rockhampton) was collected 6 September. These data indicate that reproduction is coincident with summer at least in the southern part of the range but may begin earlier in the north.

Comparison with similar species. Only six skink taxa in Australia have the upper secondary temporal overlapped by the lower – some *Calyptotis* (*C. lepidorostrum*, *C. ruficauda*, *C. scutirostrum*), some *Coeranoscincus* (*C. frontalis*), *Ctenotus*, *Lerista*, *Notoscincus*, and two species of the *Eulamprus tenuis* complex (*E. martini*, *E. frerei*). The latter two species can be readily distinguished from the *Calyptotis* by their seven supralabials and two loreals versus six supralabials and one loreal; from the *Coeranoscincus* by their five digits instead of limblessness; from *Ctenotus* by their lack of well-developed auricular lobules, and from *Lerista* and *Notoscincus* by their scaly, as opposed to windowed or spectacled eyelids.

Eulamprus martini and *E. frerei* can be most readily distinguished by their paravertebral scale count (55-64 versus 69-74) and nuchal colour pattern (a series of paravertebral blotches versus a dark midline streak).

Eulamprus tenuis (Gray)

Fig.6

Tiliqua tenuis Gray, 1831: 71 (type locality - Australia; holotype - BMNH 1946.8.17.15).

Fig.6. *Eulamprus tenuis* from Chichester State Forest, NSW.

Lygosoma erucata Duméril & Bibron, 1839: 726 (type locality - Australia; holotype - MNHP 7035).

Material examined. All localities are in New South Wales unless noted otherwise.

AM (all localities in NSW unless stated otherwise) R 1102 - Tumut; R 1135, 16115 - near Sydney; R 1911 - Penrith; R 2339 - Dobroyd; R 2999 - Hurstville; R 4001-02 - Guntawang; R 4003-5 - New South Wales; R 5955, 47200-05, 47209-11, 47214, 47217, 113126 - Sydney; R 6128, 47231 - Gerrigong; R 6279 - Gurravembi, near Macksville on Nambucca River; R 6471 - Clarence River; R 7253 - locality unknown; R 8391 - Hazelbrook; R 10930 - Canibewarea; R 11677 - Kaimkillenbru, Moola, Qld; R 14977 - Warrumbungle Mountains; R 15881 - Hammondville; R 19263 - Parramatta; R 19264 - Royal NP, Sydney; R 26014 - Connells Point, Georges River; 27359 - Childers District, Bundaberg, Qld; R 27556 - Baulkham Hills; R 27969, Hunters Hill; R 31823 - Watagan Mountains, Cessnock; R 32614 - Upper Allyn; R 41799 - Mosman; R 45303, 47218, 47220-22, 58119-20, 58122 - Earlwood; R 45807 - Balmoral; R 46046 - New Foundland SF, 16.1 km north of Woolgoolga; R 46050 - 8 km west of Douglas Park; R 47104 - Five Day Creek; R 47133 - 24 km north-east of Manilla-Retreat; 47206 - Silverwater, near Parramatta River; R 47207, 47213 - Greystanes; R 47208 - Pendle Hill; R 47212 - Baulkham Hills; R 47215 - Woronora Dam; R 47216 - Cremorne; R 47219 - Undercliff; R 47223 - Mosman; R 47230 - Mount Glorious, Qld; R 47652, 47663-65, 48102 - Bulburrin SF, Qld; R 47686, 47688-93, 48100 - Eurimbula via Miriam Vale (site 4A in rainforest survey); R 49865-67 - Lady Elliot Island, Qld; R 54280 - Murwillimbah; R 55548 - Milton; R 58118 - 2.4 km west of Putty Road on side road to Putty; R 58121 - 29 km south of Singleton on Putty Road; R 58123 - Neutral Bay; R 58431 - 2.4 km west of Appin; R 58452 - 7.4 km from Appin on Campbelltown Road; R 58453 - Three Rivers Station, Borambil; R 58454 - Elizabeth Bay, Sydney; R 58455 - near Asquith, Sydney; R 58456 - Concord, Sydney; R 58457-9, 58462, North Strathfield, Sydney; R 58460 - 18.5 km from Nymboida on Tyringham Road; R 58461 - Tooloom Falls; R 58463-64 Kilbride; R 58465, 58473; Warrawee, Sydney; R 58466 - O Bil Bil Creek, 16.1 km north-west of Mundubbera, Qld; R 58474 - Duffys Forest, Sydney; R 59995 - Austral; R 61593 - Conondale Range, Qld; R 61594-96 - Blackall Range, Qld; R 71977 - Doyalson; R 76040 - Castle Hill; R 80167 - Padstow Heights; R 81785 - Coloul track from Putty Road; R 84988 - 2.3 km south-west of junction of Mosman and Boyne Roads, Bulburrin SF, Qld; R 86286-87 - 2.4 km west of Highway No. 69 along Putty Road; R 86358 - 11 km north of Wilberforce near Highway No. 69; R 93925, 103119 - Lower Portland; R 94968 - 8.7 km north, 9.5 km east of Bega; E 96444 - Mount Warning; R 96922 - Lionsville fire trail, 6 km north of the Sugarloaf, Washpool SF, R 97666 - 9.7 km north, 7 km east of Bega; R 98679 - Dundas (Sydney suburb); R 99457 - Bardwell Park; R 103171 - Waterfall; R 103220 - St Johns Park, 4.5 km west-north-west of Canley Vale; R 103221 - 6.5 km west of Fairfield; R 103330 - Warwick Farm, Sydney; R 103343 South Greystanes; R 104973 - Maroota SF; R 106546 - 2.5 km west-north-west of Castle Hill; R 106578 - 3 km north-east of Maraylya; R 106615 - Mumbulla SF, Bega; R 107249-50 - Gordon; R 107985 - Nepean Hall, Werombi Road, near Cobbitty; R 107988 - Rozell; R 111602 - Broken River, Eungella, Qld; R 111606 - Mount Glorious, Qld; R 115285 - Eungella, Qld; R 118639 - Gladesville, Sydney; R 120576 - Cape Hillsborough, Qld; R 130869 - Dome Mount area, Yabbra SF; R 130874 - Cambridge Plateau Flora Reserve, Richmond Range SF; R 130913 - Yabbra SF

MNHP 7035 - Australia (holotype of *Lygosoma erucata*).

QM (all localities in Queensland unless stated otherwise): J1721 - South Ladevak ?; J 1728 - Qld; J 1808 - North Qld; J 2210 - Eidsvold; J 3028-29, 12119, 35398 - Mount Tamborine; J 3890 - Holbourne Island; J 4148 - Botanic Gardens, Rockhampton; J 4149 - Rockhampton; J 6233, 7926-27, 86301-31, 9598 - Brisbane; J 7925 - gardens, Brisbane; 8630-31, J 10527 - Toowoomba; J 12123-24 - Lady Elliott Island; J 12125 - 16 km south of Maryborough; J 12126 - North Sydney, NSW; J 12131-32 - Balmain, Sydney, NSW; J 15605 - Cordalba SF, 40 km south-west of Bundaberg; J 15879 - Museum gardens, Brisbane; J 17573 - Museum building, Brisbane; J 21998 - Mount Condeaux; J 23699 - Mount Glorious; J 23809 - SF 67, Bulburin, via Lowmead; J 23827 - 3.5 km north of Lowmead; J 24073 - Dunwich, North Stradbroke Island; J 27306 - Maleny; J 27389-90 - Cooloola NP via Gympie; J 27728 - Cold Creek, via Imbil; J 27733 - Dingo Creek, via Traveston; J 27743 - Marys Creek, via Gympie; J 27756 - top of Blackbutt Range, Benarkin; J 28250, 28307 - Cooyar/Maidenwell Road; J 28357-58; 33624, 33632-33634 - Bulburin SF; J 28790 - Hinchinbrook Island; J 30773 - Jimna, Yabba Top Road; J 31307 - Burnett Range via Tansey; J 31698 - Finch Hatton Gorge, Eungella NP; J 31844 - Glastonbury near Gympie; J 33603, 33677-78, 33680, 33696 - Site 1 A, Bulburrin SF; J 33625, 33633 - Bulburin SF; J 33772 - adjoining site 5, Rundle Range; J 34067, 34074, 34083 - adjoining site 9, Finch Hatton NP J 34091 - site 9A, Finch Hatton, NP; J 34126 - 8.1 km north of Toowoomba; J 34302-04 - Mimosa Creek, Blackdown Tableland via Dingo; J 34323 - Qld Museum; J 35126 - SF, 1 km south of Broken River NP; J 35268 - Burgowan Minesite No. 13, east of Howard; J 35269, 35276 - Ferguson SF via Maryborough; J 35293 - Dundowran; J 36062 - Kauri Creek Inlet via Gympie; J 38621 - Nathan Gorge; J 38680 - "The Battery" via Glenhaughton; J 39106 - Churchill Mine Road, Maryborough; J 39183 - south-west end of Goodnight Scrub; J 39608-09 - Kroombit Tops SF, 30 km west-south-west of Nagoorin via Monto; J 39986, 39994 - Eurimbulah Beach, 32 km north-east of Miriamvale; J 41540 - Pine Creek Timber Reserve (102), south of "Turkey", Miriam Vale; J 42130 - Kroombit Tops, Upper Dry Creek; J 42194 - Worthington Creek, via Turkey Station via Miriamvale; J 46174 - Eungella schoolhouse.

QNPWS: R 161 - Cunninghams Gap NP; R 344-45 - Toolara SF (between Gympie and Tin Can Bay); R 379 - Girraween NP; N 11123 - Broken River, Eungella NP; N 11218 - Collaroy Pastoral Holding (south of Sarina); N 15899 - Eungella NP; N 17673 - Finch Hatton Gorge, Eungella NP.

Diagnosis. Differs from all other members of the *Eulamprus tenuis* complex in the following combination of characters: upper secondary temporal overlaps lower; transversely enlarged nuchals 0-4, mode 2; subdigital lamellae fourth toe 22-27; nuchal area often with dark midline streak.

Distribution. From Holbourne Island and the Eungella region in central eastern Queensland south to just north-east of Bega (Lunney & Barker, 1986) in south-eastern New South Wales; inland as far as the Warrumbungles and off the coast on Lady Elliott Island (Fig.9).

Habitat. Associated with forest in northern part of range (Czechura & Miles, 1983) and with woodland in southern part (personal observation); commensal of humans in some areas.

Habits. Arboreal and saxicolous; diurnal, crepuscular, and nocturnal; heliothermic but usually only in filtered or patchy sunlight.

Reproduction. Ovoviviparous. Females carrying yolking follicles or developing oviducal young range 70 to 84 mm (mean = 76.8; *sd* = 3.82; N = 15) SVL. Those with countable eggs or young range 70 to 84 mm (mean = 77.2; *sd* = 3.75; N = 13) and have litter sizes three to seven (mean = 5.4; *sd* = 1.39); there is no significant correlation between female size and follicle number/litter size in these females (r = -0.14NS).

Dates of collection are available for 11 gravid females collected in the area from Sydney to Brisbane. Four of these females have enlarged yolking follicles and were collected in the period late August to January. The one January animal, which represents a late date, was from the southernmost locality, Sydney. The remaining seven females carry developing young. These females were collected in the period September to late December. The one September animal, which represents an early date, is from the northernmost locality, Brisbane.

Variation. Some individuals in the relatively dense population in and around Taronga Park Zoo in Sydney are light brown to beige with little or no indication of pattern. They are indistinguishable morphologically from normally patterned individuals.

Eulamprus sokosoma n.sp.

Figs 7-8

Type material. HOLOTYPE, QM J 27702 - Hencamp Creek, 5 km north, 1 km east of Rollingstone, Qld, 30 May 1976, F. Parker.

PARATYPES (all localities are in Queensland): AM R 49858 - Bailey Islet; R 49859, 49861 - Bay Rock, near Townsville; R 61601 - Arcadia Valley via Injune; R 86304-16, 113882-83 - 29.1 km west-south-west of Ross River Road

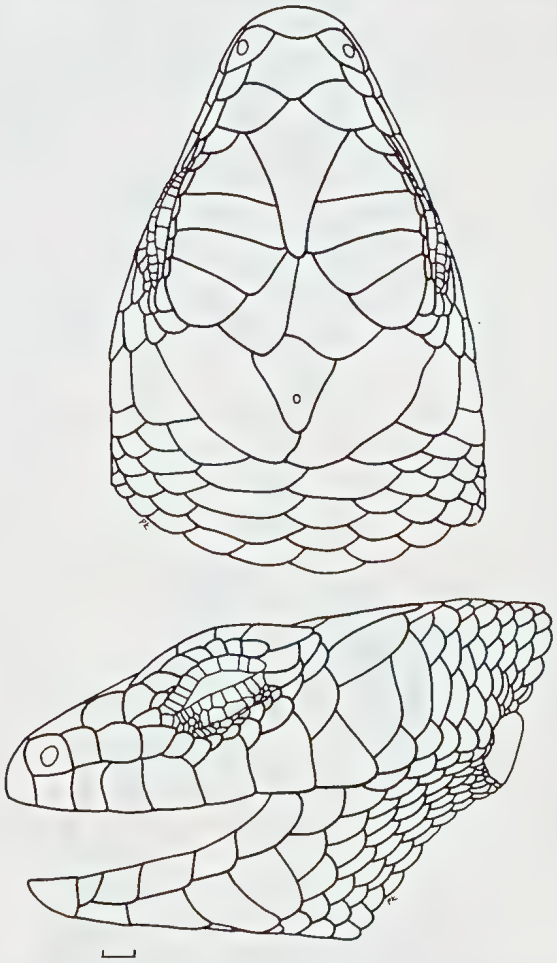

Fig.7. *Eulamprus sokosoma* n.sp. (AM R 86309) from the eastern slopes of the Harvey Range just west of Townsville, Qld. Bar scale = 1 mm.

Fig.8. *Eulamprus sokosoma* (holotype QM J 27702) from Hencamp Creek 5 km north, 1 km east of Rollingstone, Qld.

(Townsville) via Harvey Range Road.

QM J 15668 - Yebna Station, 80 km east of Injune; J 25915 - Arcadia Valley via Injune; J 27622-23 - Hervey Range, 10 km south, 35 km west of Townsville; J 33843 - site 5A, Rundle Range; J 34209 - halfway up Blackdown Tableland escarpment, via Dingo; J 42506 - Many Peaks Ridge, Townsville Common; J 42513 - Blue Water Range, north of Townsville; J 42516-17 - Hervey Range west of Townsville; J 42526 - Fanning River Caves near Mingela.

QNPWS N 1787 - Taravale Road (behind Mount Spec NP); N 36821 - Hoven's Hole Cave entrance, Fanning River Station.

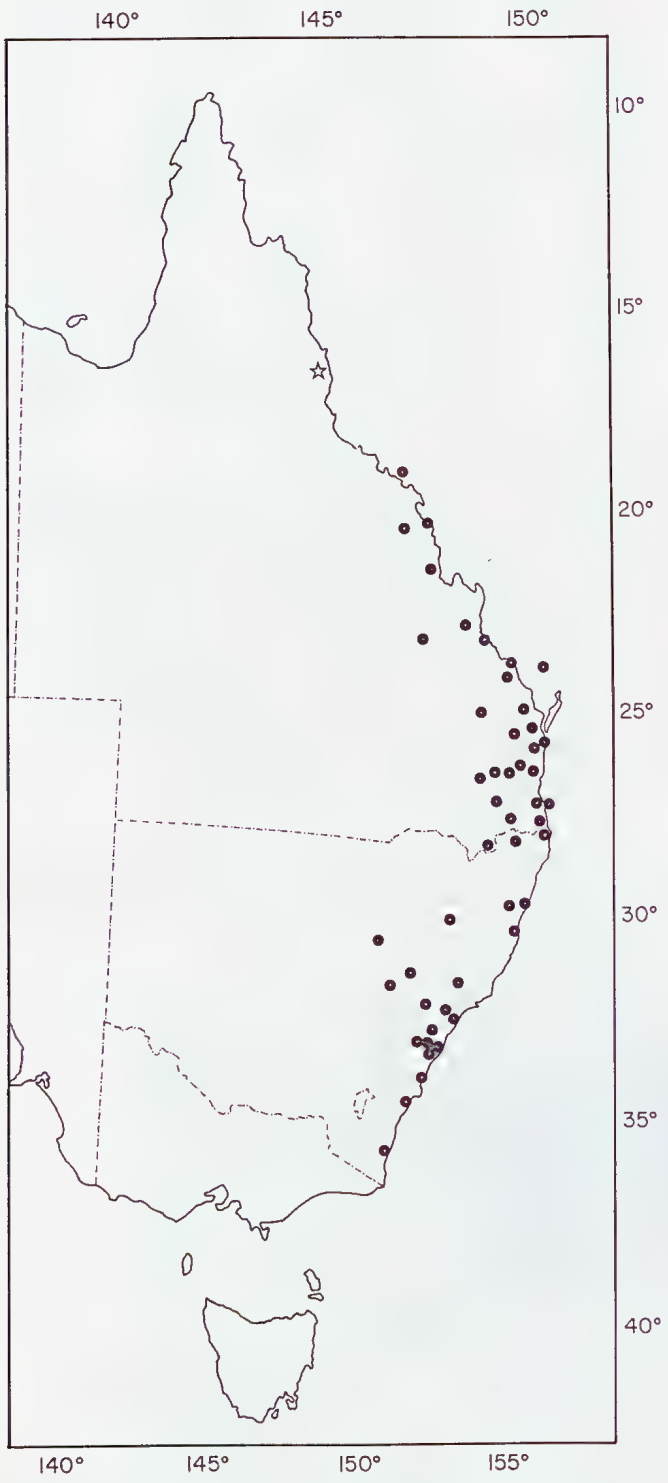

Fig.9. The distribution of *Eulamprus tenuis* (closed circles) and *E. frerei* (star).

Diagnosis. Differs from all other members of the *Eulamprus tenuis* complex in the following combination of characters: upper secondary temporal overlaps lower; transversely enlarged nuchal scales total 2-8, mode 4; subdigital lamellae (fourth toe) 19-23; nuchal area without dark midline streak; midbody scale rows 32-38.

Distribution. Known only from scattered localities in central eastern Queensland between the Townsville area in the north and the Injune area in the south (Fig.5).

Habitat. Closed vine thickets along east-facing gullies (Harvey Range).

Habits. Arboreal and saxicolous; retreating into crevices; diurnal; heliothermic in filtered or patchy sunlight.

Reproduction. Ovoviviparous. None of the three females (SVL = 52, 77 and 78 mm) collected 16 May 1976 at the Harvey Range locality were reproductively active but the two (SVL = 71-72 mm) collected here on 30 September 1985 carried, in one case, yolking follicles (too mashed to count) and in the other, four developing, oviducal young. These data indicate that female reproduction is curtailed during the mid-dry season but recommences toward the end of the dry season.

Details of holotype (QM J 27702). prefrontals narrowly separated; supraciliaries 8/8; presuboculars 2/2; supralabials 7/7, fifth subocular on both sides; nuchals 3/3 = 6; infralabials 6/6; longitudinal scale rows at midbody 32; paravertebral scales 62; subdigital lamellae on fourth toe 19/19; SVL 74mm; front limb length 19 mm; hind limb length 26 mm; tail length 87 mm of which 7 mm is regenerated; sex female.

Comparison with similar species. See comments under this section in the *Eulamprus brachysoma* account.

Etymology. From the Greek for stout (*sokos*) and body (*soma*) and alluding to the characteristically robust body of the species.

Eulamprus frerei n.sp.

Figs 10-11

Type material. HOLOTYPE, QM J 47985 - summit of Mount Bartle-Frere, Qld, J. Covacevich, 27 Oct. 1987. PARATYPE, QM J 39531 - Mount Bartle-Frere summit, Qld.

Diagnosis. Differs from all other members of the

Fig.10. *Eulamprus frerei* n.sp. (holotype, QM J 47985) from Mount Bartle-Frere, Qld.

Eulamprus tenuis complex in having the upper secondary temporal overlapped by the lower and 69-74 paravertebral scales. The species also differs from all other members of the *E. tenuis* complex in having the dorsum uniform brown with contrasting finger-like crossbands from the dark brown to black dorsolateral stripe broken into mid-dorsal bands (holotype) or spots (paratype); other species have the dorsum grey to light brown with a series of dark bands along the paravertebral area or a more general dark mottling (Fig.10). It also seems to differ from other members of the *E. tenuis* complex in having the subdigital lamellae only lightly pigmented instead of usually heavily pigmented.

Distribution. Known only from the summit of Mount Bartle-Frere (Fig.9).

Habitat. The summit of Mount Bartle-Frere consists of large fields of granite boulders surrounded by dense rainforest; the area is cool to cold throughout the year and is frequently covered in mist (Covacevich, 1984).

Habits. The holotype was collected from the crevice of a dead tree at 1000 hours.

Reproduction. Nothing known.

Comment. This is the second apparent endemic to the summit of Bartle-Frere, the other being *Leiolopisma jigurru* Covacevich, 1984. These two species, along with *Calyptotis thorntonensis* from the top of Thornton Peak in north-eastern Queensland and *Pseudemoia palfreymani* from the island of Pedra Branca south of Tasmania, are the four most geographically restricted lizards in Australia.

Details of holotype (QM J 47985). Prefrontals slightly separated; supraciliaries 8/8; presuboculars 2/2; supralabials 7/7, 5th subocular on both sides; infralabials 6/6; subdigital lamellae on fourth toe 27/25; SVL 66 mm; front limb length 21 mm; hind limb length 30.5 mm; tail length 82 mm (tip only regenerated?); sex male.

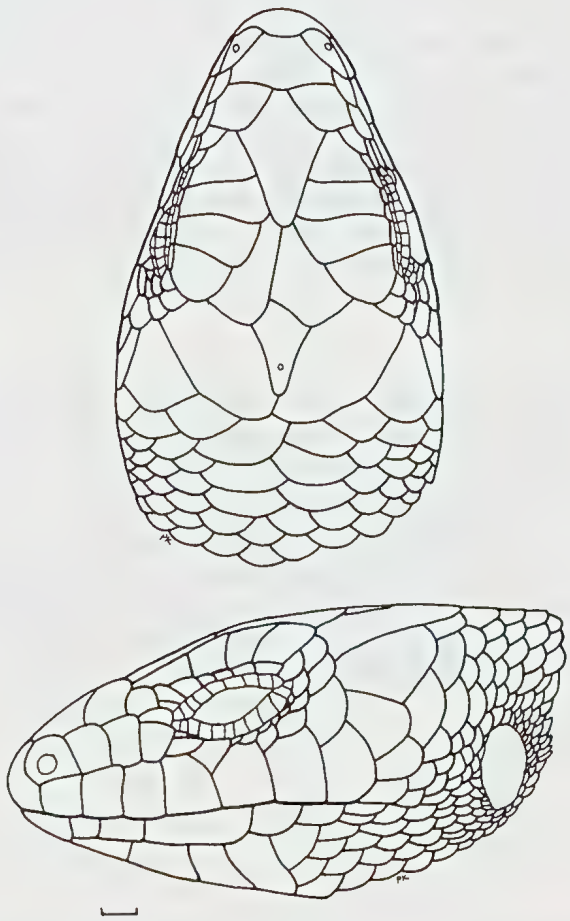

Fig.11. *Eulamprus frerei* n.sp. (holotype, QM J 47985) from Mount Bartle-Frere, Qld. Bar scale = 1 mm.

Comparison with similar species. See this section under *Eulamprus martini*.

Etymology. Named after the type and only known locality of the species.

Comments on the Distribution of the Species in the Eulamprus tenuis *Complex*

All the species in the *Eulamprus tenuis* complex have the main parts of their contiguous distributions close to the mesic east coast (Figs 2, 5, 9). Inland populations are usually isolated and associated with slightly uplifted or dissected terrain where there are likely to be local pockets of more mesic habitat. Presumably these inland populations are relicts of a more generally mesic time in the past.

Although there is potential for several species to occur in broad sympatry, e.g., *Eulamprus brachysoma* and *E. sokosoma* in north-eastern Queensland; *E. brachysoma*, *E. martini* and *E. tenuis* in south-eastern Queensland; and *E. martini* and *E. tenuis* in far south-eastern Queensland and north-eastern New South Wales. The only records to date of local sympatry are for *E. martini* and *E. tenuis* in far south-eastern Queensland (Czechura & Miles, 1983). Here *E. martini* (as *E. brachysoma*, G. Czechura, *in litt.*) inhabits open forest and woodland whereas *E. tenuis* occupies dense eucalypt forest and rainforest.

ACKNOWLEDGMENTS. I thank T. Goh and J. Nancarrow for typing; P.A. Koshland for artwork (Figs 3, 7, 11), and J. Covacevich, G. Czechura and K. McDonald for critically reading versions of the manuscript.

I would like to acknowledge that I came late to the taxonomic problems dealt with here. Those that had insight into various aspects of the problem before me were: G. Czechura, J. Covacevich, D. Knowles, K. McDonald, P. Rankin (deceased) and S. Wilson. I have benefited greatly from their knowledge and generosity.

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Table 1. Mensural and meristic characters for *Eulamprus tenuis* and the four species most similar to it. The species are ordered from left to right by increasing maximum size.

Character	*E. frerei*	*E. martini*	*E. brachysoma*	*E. sokosoma*	*E. tenuis*
Midbody scale rows					
Range	32-35	28-32	28-32	32-38	28-32
Mean	33.5	29.5	30.4	35.1	30.1
SD	–	1.19	1.25	1.48	1.07
N	2	20	25	30	31
Paravertebral scales					
Range	69-74	55-64	56-67	59-72	61-69
Mean	71.5	58.6	60.5	66.6	65.1
SD	–	2.80	2.98	3.50	3.11
N	2	17	20	30	12
Subdigital lamellae					
Range	24-27	18-24	17-23	19-23	22-27
Mean	25.5	20.7	20.0	21.1	23.6
SD	–	1.35	1.39	1.14	1.41
N	2	21	28	30	31
SVL (mm)					
Range	66	23-71	26-74	52-79	30-86
N	2	120	78	30	82
TL/SVL (%)					
Range	–	123-171	121-151	–	110-146
N	2	23	7	30	10
Nuchals (total)					
Range	6-7	0-8	2-10	2-8	0-4
Mean	6.5	5.2	6.0	4.7	2.2
Mode	6/7	6	6	4	2
N	2	61	66	27	59
Premaxillary teeth					
9	–	2	6	4	5
8	1	2	1	–	–
7	–	5	–	–	–
Vomers (N)					
distinct	–	10	5	2	–
fused	1	–	–	–	4

Fossil Avian Assemblage of Pitfall Origin from Holocene Sediments in Amphitheatre Cave (G-2), South-western Victoria, Australia

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ABSTRACT. The fossil avian assemblage from Amphitheatre Cave (6 km north of the township of Nelson, Victoria, Australia) consists of 27 species of birds. Three dominate the assemblage with 63% of the total minimum number of individuals (i.e., *Gallinula mortierii*, *Dasyornis broadbenti* and *Dasyornis brachypterus*). Most of the material originated from a pitfall accumulation, based upon the large percentage of individuals belonging to terrestrial species with elements lacking the damage characteristic of vertebrate accumulators. Geographic range extensions are noted for three species (i.e., *Gallinula mortierii*, *D. brachypterus* and *Ptilonorhynchus violaceus)*. Assuming the assemblage is intra-contemporaneous, the reconstruction of vegetation at the time of deposition would include; wetlands with some areas of short cropped grass, bordered by wet heathland, which subsequently gave way to *Eucalyptus* open forest formation away from the water source and *Eucalyptus* tall open forest formation in the gullies. The age of the deposit (4,670 ± 90 y.B.P.: NZA 700) is based upon a single radiocarbon date on bone.

BAIRD, R.F., 1992. Fossil avian assemblage of pitfall origin from Holocene sediments in Amphitheatre Cave (G-2), south-western Victoria, Australia. Records of the Australian Museum 44(1): 21–44.

Amphitheatre Cave (G-2: Matthews, 1985) is located approximately 6 km north of the township of Nelson, south-western Victoria (38°03'S 141°01'E) and occurs in the central part of an easterly facing cliff, approximately 15 m above the Glenelg River.

The exact location of the cave from which this material came, was unknown for a number of years, and it was therefore referred to by the name of the collector of the fossil material, F.S. Colliver (i.e., Colliver's Cave: Rich & Baird, 1986; Baird, 1986). Recently a foray was organised, through the help of the Department of Conservation Forests and Lands, where the author was able to view cave entrances from the river. At this time the cave was confirmed as being the southern entrance of Amphitheatre Cave (G-2), matching a photo of the cave entrance provided in Colliver's (1938) article on

the deposit (see Fig.1). Note that the entrance to the cave is actually below that indicated by Colliver, and that the area he indicated is only shadow produced by a small overhang.

"Cave has three entrances to high bifurcating joint controlled passage 80 m long, 18 m deep. Main chamber has large aven. Two entrances are joint enlargements in cliff face 15 m above river level, third entrance is enlarged solution tube 30 m deep x 1.5 m diameter." (Davey & White, 1986).

See Figure 2 for a plan view and position of excavation within the cave.

The excavation was started by F.S. Colliver on April 20 and 21, 1935 (Easter weekend), and completed over three subsequent trips (Colliver, 1938). The material was collected by bringing "...handfuls of the flour [sediment within the cave] at a time and spread it on the surface within a daylight area, and picked out any small bones, jaws or individual teeth that appeared. The bigger bones were felt within the flour and gently eased out" (Colliver, personal communication).

The cave occurs on the Follett Coastal Plain (Land Conservation Council, 1981) of south-western Victoria. This region is characterised by a dissected coastal plain with a variation in elevation between 0 to 60 m. Subparallel consolidated limestone ridges trend north-west to west-north-west, with inter-dune corridors between 2 to 11 km wide. These are thought to mark former Pleistocene shorelines. Sandsheets of orange siliceous sand are widespread.

The local climate consists of rainfall with a winter maximum of 112 mm and a summer minimum of 28 mm (average rainfall) and temperature ranges from 3.6 to 13.7°C (range of mean monthly temperatures) in June to 10.8 to 25.2°C in January, based upon the rainfall and temperature curves of the nearest weather station in Rennick, Victoria (approximately 19.5 km north of Amphitheatre Cave). Westerly winds predominate.

The local vegetation consists largely of woodland or open forest, composed of brown stringybark (*Eucalyptus baxteri*), messmate (*E. obliqua*), manna gum (*E. viminalis*), shining peppermint (*E. nitida*) and swamp gum (*E. ovata*), with extensive heaths as understorey. In the immediate vicinity of the cave the vegetation is a mixture of open scrub, heathland and open forest (Land Conservation Council, 1981). For a history of vegetation changes in the area refer to Baird (1985).

Material and Methods

The material reported on herein was gleaned from several drawers of material in the Museum of Victoria, Department of Vertebrate Fossils, labelled as collected by F.S. Colliver from Amphitheatre Cave, Glenelg River region (see Introduction). To the best of my knowledge all of the avian material available has been studied, though for some taxa, only higher taxonomic level determinations are presented. Modern comparative material used in the identifications was provided by the Department of Ornithology, Museum of Victoria and Department of Ornithology, South Australian Museum.

All of the fossil material discussed will be deposited in the Museum of Victoria, Department of Vertebrate Fossils. Museum of Victoria catalogue numbers can be found in the Materials section of each species account. A prefix 'P' should accompany each number but has been omitted for conservation of space.

The Scientific names used in each account follow Condon (1975) and Schodde (1975). Taxa previously unknown from sub-fossil and fossil deposits are noted (unpublished records in the faunal lists of Rich & van Tets (1982) are not considered formally confirmed

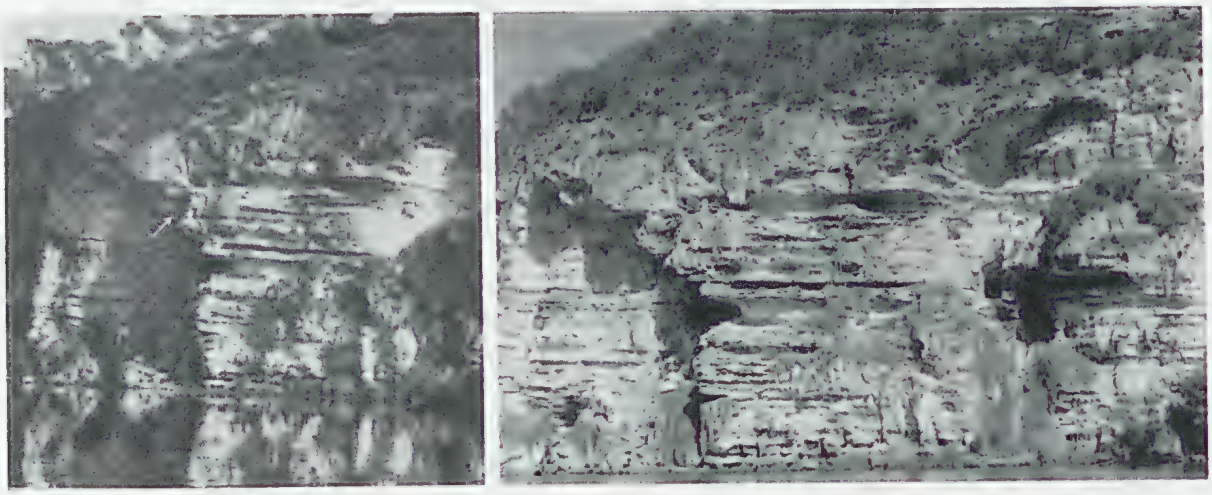

Fig.1. Photographs of the entrance to Amphitheatre Cave, including the original from Colliver (1938) and a more recent one taken by the author. Note that in the original photo the arrow only points to a small overhang, in the new photo both the south and the north entrances can be discerned. The south entrance is 15 m above the water level.

records as no full diagnoses are provided). Minimum numbers of individuals were determined by the standard method of counting the most abundant element from a particular side.

Geographical ranges for each species are here assumed to be the same as the current range, unless otherwise noted. The current range of each species is assumed to include the area surrounding the amphitheatre section of the Glenelg River, unless mentioned otherwise.

Anatomical terminology follows Baumel *et al.* (1979).

All measurements in the text are in millimetres. Standard measurements in the text are indicated in brackets and follow the guidelines in von den Driesch (1976) unless stated otherwise. All measurements were taken with vernier callipers accurate to 0.05 mm and were rounded to the nearest 0.1 mm.

Species determination is based upon mensural criteria in every species account except where otherwise stated. Botanical nomenclature follows the guidelines of Specht (1981).

All tables referred to throughout the paper are included in Appendix I. Abbreviations used in the text, figures and appendices are listed in Appendix II.

Material identified as juvenile is based upon the criteria of having a "...pitted appearance of the surface of the bone and incomplete ossification of the articular facets..." (Campbell, 1979: 17).

Morphological characters for determinations higher than species level are included in Appendix III, unless only one element is considered, in which case they are included in each species account. Characteristics include those separating the species from closest relatives and other families which may have similar appearance to the elements in question. This is not supposed to be an exhaustive account of characters separating the species, families and orders in question but only a guide to the characters used to identify the elements in question from all other Australian taxa with similar appearance. All bird species currently recorded from the Australian continent and Tasmania were included in the comparisons unless noted otherwise (in the Characters section of the species accounts).

Unless otherwise stated, actualism or methodological uniformitarianism is assumed to be valid (see Simpson, 1970 and Gould, 1965, 1985, respectively). This implies that if a species is restricted to a particular set of environmental parameters currently, the species was also restricted to those parameters in the past. Although there are several examples of modern species, now restricted to specific habitats, that are found in deposits whose faunal composition suggests that those species inhabited a wider range of habitats in the past than is presently displayed, I have not presumed wider ecological tolerances for species unless the fauna, as a whole, or

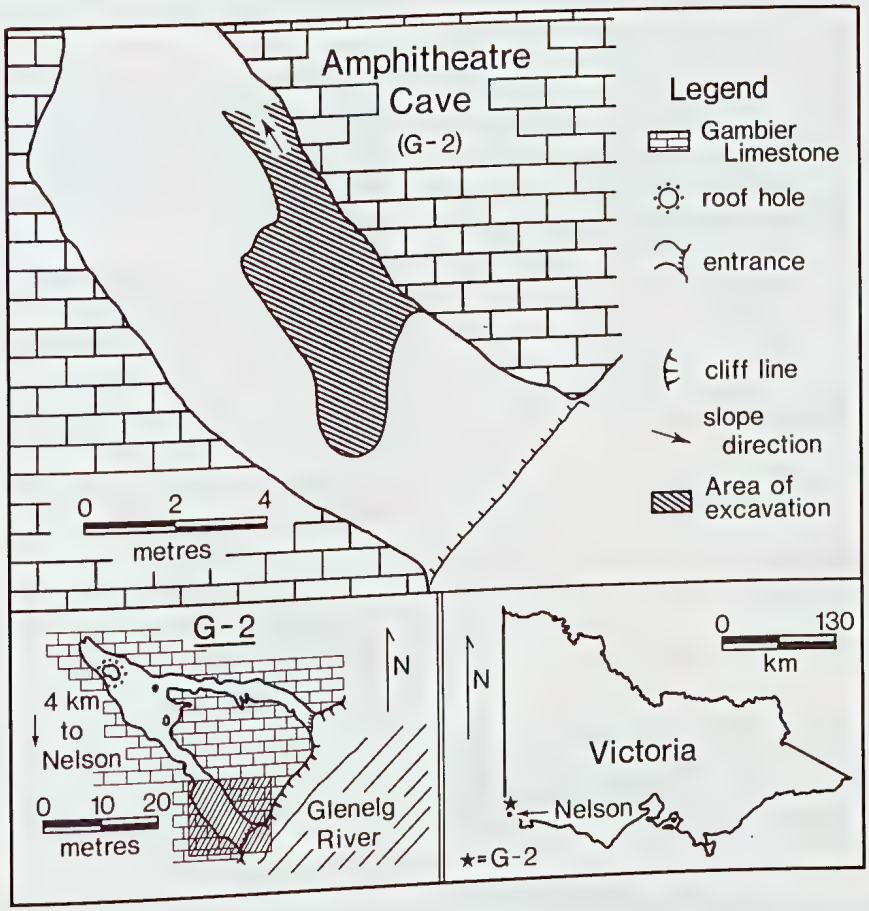

Fig.2. Plan view of Amphitheatre Cave demonstrating the position within the feature from which the fossil material was excavated.

palaeobotanical information suggests otherwise. Information provided in the environmental reconstructions is based on species habitat preferences from modern analogues (see Baird, 1989).

Systematic Palaeontology

Aves

Sphenisciformes

Spheniscidae

Eudyptula minor

Material. prox. frag. pel. (178677), com. right fem. (178678), com. left fem. (178679), incom. left tbt. (178680), incom. left tmt. (178681).

Characters. *Eudyptula minor* is the smallest extant penguin in the world, and the fossil material conforms to the range of variation exhibited by this species.

Remarks. The condition of the material referred to this species differs from that of most of the material from this cave in that it is bleached white with sand grains adhering to their surfaces. Elements with similar preservation are those referred to *Pachyptila* sp., *Phalacrocorax* sp. and *Larus novaehollandiae* (see Taphonomy section for more details). This species is largely pelagic, but is known to have colonies along most of the southern coastline of Australia (Serventy *et al.*, 1971) and beach washed specimens are frequent in the south-east of South Australia (Parker & Reid, 1983).

Procellariiformes

Procellariidae

Pachyptila sp.

Material. incom. right ulna (178682).

Characters. The two characters on the ulna considered diagnostic for the family Procellariidae, include: Ulna (whole), 1. shaft markedly straight and angular, 2. *cot. ventralis* and *cot. dorsalis* proximally facing.

The element is referred to the genus *Pachyptila* based on its diminutive size.

Due to the amount of mensural overlap, the extant species of *Pachyptila* cannot be separated by mensural criteria of the ulna; therefore, the determination is *Pachyptila* sp. (see Olson, 1985 for a discussion and figure of *Pachyptila* ulnae).

Remarks. See Remarks section for *Eudyptula minor*.

Pelecaniformes

Phalacrocoracidae

Phalacrocorax sp.

Material. 2 incom. pel. (178683, 178684).

Characters. The suite of characters on the synsacrum considered diagnostic for the family Phalacrocoracidae, include: Synsacrum, 1. *cta ventralis* markedly expanded ventrally, 2. long and gracile throughout, 3. no opening for proximodorsal canal, distally, 4. tubercles present just dorsal to the *antitrochanter*.

The Australian species of *Phalacrocorax* can be separated into three size groups. The fossil material agrees in size with the medium-size group, which includes both *P. fuscescens* and *P. varius*. Due to extensive mensural overlap within this a group species-determination cannot be finalised.

Remarks. For colouration and other surficial characters see that under *Eudyptula minor*. Habitats include marine, coastal, subcoastal lakes, and inland waters (Parker & Reid, 1983).

Anseriformes

Anatidae

small species

Material. incom. right ccd. (178685), incom. right tbt. (178609).

Characters. Generic and specific determinations are not considered possible due to the small amount of comparative material currently available.

Accipitriformes

Accipitridae

Accipiter fasciatus

Material. com. left tmt. (167068).

Characters. The suite of characters considered diagnostic for the genus *Accipiter* includes: Tarsometatarsus, (proximal end), 1. *cta medialis* and *lateralis* completely separate with a small groove on the lateral edge of *cta lateralis*, 2. *imp. retinaculi extensorii* are positioned on the medial edge of the dorsal surface close to *cot. medialis* and *lateralis*; (distal end), 1. laterally compressed shaft, 2. laterally compressed *troc. metatarsi terti*, 3. dorsal surface of *troc. metatarsi secundi* slopes gently medially, viewed distally, 4. *troc. metatarsi* nearly equal in length, 5. *fora. vascularia* distale further proximal than most other accipitrids; 6. *troc. metatarsi secundi* and *terti* does not extend as far ventrally.

Species determination is based upon size where *Accipiter fasciatus* is consistently less robust than *A. novaehollandiae*, and the dimensions of the fossil specimen (e.g., G.L. = 77.9, B.p. = 9.3) fall within the range of variation exhibited by *A. fasciatus* (see Fig.3).

Remarks. According to Blakers *et al.* (1985) *Accipiter fasciatus* "...lives wherever there are groves of trees but is most abundant in forest and woodland".

Falconidae

cf. *Falco cenchroides*

Material. incom. right ulna (167255).

Characters. The suite of characters diagnostic for the genus *Falco*, include: Ulna, (proximal end), 1. *cot. ventralis* dorsoventrally flattened, 2. *olecranon* dorsoventrally flattened, 3. *dep. M. brachialis* prominent and extends distally, 4. distinct ridge leading to *olecranon* proximally (viewed posteriorly); (shaft), 1. curved (convex posterior); (distal end), 1. *labrum condyli* extends proximally, 2. *tub. carpale* large and curved ventrally.

Species determination is based on overall size, precise measurements are not considered reliable due to damage of the terminal ends.

Remarks. *Falco cenchroides* occurs throughout Australia and is capable of surviving in all terrestrial habitats.

Galliformes

Phasianidae

Coturnix sp.

Material. incom. rost. (178686), incom. right hum. (167251), com. left hum. (167246), dist. end left hum. (167248), 2 com. right ulna (167219, 167257), com. left ulna (178687), 2 com. right ccd. (178383, 178386), com. left ccd. (178509), huml. end left scap. (178381), incom. right tmt. (167294), incom. right tmt. (juv.)(178619), com. left tmt. (167237).

Characters. The larger species of *Coturnix* cannot be separated by size or morphology (see Baird, 1986).

Remarks. Of the two species considered to be biogeographically likely for this material, *C. australis* and *C. pectoralis* are both irruptive. They disperse when

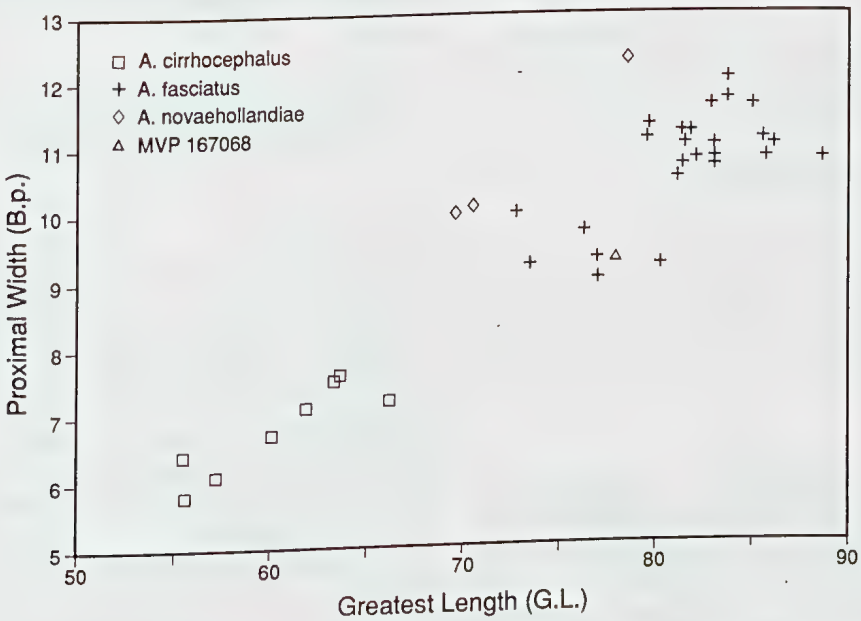

Fig.3. Plot of tarsometatarsi measurements of modern comparative specimens from the three species of *Accipiter* occurring in Australia, as compared with the fossil specimen from Amphitheatre Cave (167068), demonstrating the affinity of the specimen with *A. fasciatus*.

food becomes scarce, and *C. pectoralis* will invade inland areas after substantial rains (Frith *et al.*, 1977; Frith & Waterman, 1977); therefore, the range of habitats covered by these species is large and includes EOFF, EWF, HF, MOSF and ATSF.

Gruiformes

Turnicidae

Turnix varia

Material. 3 com. right hum. (178365-178367), 2 incom. left hum. (178615, 178616), incom. right ulna (178514), com. right ccd. (167074), com. right ccd. [juv.] (178363), com. left ccd. (178362), incom. left ccd. (178614), com. furc. (178508), stm. spin. proc. frag. (178364), incom. stm. [juv.] (167071), com. right fem. (178688), prox. end right fem., (167271), incom. left fem. (178689), com. right tbt. (167233), com. right tbt. [juv.] (178368), prox. end right tbt. (178618), com. left tbt. (178617), incom. left tmt. (178368).

Characters. *Turnix varia* is larger than all other species of *Turnix* in south-eastern Australia (see Table 1). Comparative material included only *T. melanogaster*, *T. varia*, *T. velox* and *T. pyrrhothorax* since no other Australian turnicids are represented in skeletal collections.

Remarks. The range of habitats frequented by this species includes "...eucalypt forest [EOFF], woodland [EWF], and heath [HF] where there is a layer of leaf and twig litter..." (Blakers *et al.*, 1984). In the south-east of South Australia, this species occurs in inland HF and EWF (Bourne, 1982; Parker & Reid, 1983).

Rallidae

Rallus philippensis

Material. incom. rost. (178504), com. left hum. (178592), com. right rad. (167183), com. right cmc. (167230), com. right scap. (167083), com. syn. (167182), com. right fem. (167167), com. left fem. (167103), com. right tbt. (167102), com. left tbt. (178658), com. right tmt. (167295), com. left tmt. (178452).

Characters. *Rallus philippensis* is the largest of the small rallids in Australia and the fossil specimens fall within the range of variation exhibited by this species (see Baird, 1986).

Remarks. All of the elements probably came from a single individual, as there are no duplicates of elements and measurements for each pair of postcranial elements are identical.

The habitat requirements of *R. philippensis* include wet tussock grassland (Parker & Reid, 1984), "...rank vegetation in swamps and along creeks or in paperbark woodlands..." (Blakers *et al.*, 1984), mangroves and wet sclerophyll forest [ETOFF] (Morris *et al.*, 1984).

Gallinula mortierii

Material. See Appendix IV.

Characters. Postcranial elements of *G. mortierii* are larger and more robust than those of all other species of rail in Australia (see Olson, 1975; Baird, 1984).

Remarks. The Tasmanian Native-hen, currently restricted to the island of Tasmania, is a secondary grazer and most frequently encountered in areas near permanent or temporary water, including arable land and cultivated pastures. It is dependent on short lush pasture for feeding and permanent water for breeding (Ridpath, 1972).

The mid-Holocene radiocarbon date on the *Gallinula mortierii* element from Amphitheatre Cave prompted a review of the hypotheses for its extinction from the mainland of Australia (Baird, 1991b) in which Baird argued that it is possible that both the dingo (*Canis familiaris dingoensis*) and the environment may have been important to this extinction.

Because of the abundance of *G. mortierii* in this deposit measurements for most of the postcranial elements have been provided in Appendix V to facilitate comparison with material from other fossil deposits.

Charadriiformes

Laridae

Larus novaehollandiae

Material. incom. right hum. (178690).

Characters. The suite of characters diagnostic for the family Laridae include: Humerus, (distal end), 1. long *proc. supracondylaris dorsalis*, not incurved, 2. deep *fossa M. brachialis.*

The suite of characters considered diagnostic for the genus *Larus* include: Humerus, (proximal end), 1. *caput humeri* low, 2. second *fossa pneumotricipitalis* relatively shallow, 3. *cta pectoralis* proximally located; (distal end), 1. *proc. supracondylaris dorsalis* distally located.

Larus novaehollandiae is the smallest species of

Larus in Australia and the fossil material agrees with comparative modern specimens of that species.

Remarks. For condition of preservation see that under *Eudyptula minor*.

Larus novaehollandiae is found throughout Australia, and seems only to require the presence of open water, be it fresh, brackish or salt (Blakers *et al.*, 1984).

Columbiformes

Columbidae

Phaps chalcoptera

Material. incom. right ccd. (167240).

Characters. The suite of characters considered diagnostic for the family Columbidae, include: Coracoid, (humeral end), 1. *proc. acrocoracoideus* ends, distally, very abruptly, 2. distance between *proc. acrocoracoideus* and *cot. scap.* relatively large, 3. *cot. scap.* broad and extends sternally down shaft, 4. lacks pneumatic fenestrae at interface of *sul. M. supracoracoidei* and *fac. art. clavicularis*; (sternal end), 1. *angulus medialis* attaches broadly to main body of coracoid, 2. *proc. lateralis* extends beyond *fac. art. sternalis*.

The suite of characters considered diagnostic for the genus *Phaps*, include: Coracoid, (humeral end), 1. internal edge of *imp. lig. acrocoracohumeralis* medially elongate (from an internal view, *imp. lig. acrocoracohumeralis* mainly obscured by this edge), 2. *imp. lig. acrocoracohumeralis* rectangular in outline (in humeral view), 3. *fac. art. clavicularis* medially located.

Of the three members of this genus *P. chalcoptera* is the largest, and the specimen falls within the range of variation demonstrated by that species (see Table 2).

Remarks. *Phaps chalcoptera* is the most wide-ranging species of large columbiform in Australia. This species can be found "...in all, except the most dense and wet wooded habitats" (Frith, 1982). Although it currently frequents coastal heathlands, Frith (1982) considered that this is largely the result of the clearing of eucalypt forests, whereas the heaths are usually left untouched. This, according to Frith, causes the members of this species to expand into what might be considered sub-optimal habitat.

Phaps elegans

Material. incom. left ccd. (167207).

Characters. See that under *Phaps chalcoptera* for the suites of characters considered diagnostic for the family Columbidae and the genus *Phaps*.

Of the three members of this genus *P. elegans* is the smallest, and the fossil specimen falls within the range of variation demonstrated by that species (see Table 2).

Remarks. "Throughout its [*Phaps elegans*] range, it maintains this preference for heathland and other vegetation with a heath-like structure" (Frith, 1982). This is particularly true around swamps and in coastal and sub-coastal country. Although this species is not exclusively dependant upon heaths, where it is sympatric with *P. chalcoptera*, it seems to have a strong preference for this type of habitat.

Species previously unrecorded in the fossil record.

Psittaciformes

Loriidae

Glossopsitta concinna

Material. incom. right ulna (167224), incom. left cmc. (178601).

Characters. Both generic and specific determination of based on mensural criteria. Postcranial elements of the three species of *Glossopsitta* are smaller than any of the member in the genus *Trichoglossus*. Of the three species in the genus *Glossopsitta*, *G. concinna* is the largest and the elements referred to this species fall within the range of variation for this species.

Remarks. *Glossopsitta concinna* inhabits most types of forested or wooded country (Morris *et al.*, 1981; Blakers *et al.*, 1984) and will frequent any area where "...there are flowering or fruit bearing trees or shrubs..." (Forshaw, 1969).

Cacatuidae

Cacatua tenuirostris

Material. incom. right hum. (178657).

Characters. The element conforms to all those morphological characters for *C. tenuirostris* defined in Baird (1985), including: 1. presence of a small posterior groove on anterior face of *cta pectoralis*, 2. a deep *fossa pneumotricipitalis*, and 3. a greater angle between *inc. capitis* and shaft axis. Mensurally, the total length [GL = 71.6] falls just above the mean for the modern comparative material [GL = 71.3] and well below the

mean of the fossil population of this species in Green Waterhole Cave (GL = 74.6; Baird, 1985).

Remarks. Emison & Beardsell (1985) define the habitat of *C. tenuirostris* as EWF, especially those composed of River Red Gum (*Eucalyptus camaldulensis*) woodland alliance (85%) with an additional small percentage of sightings (15%) in South Australian Blue Gum (*E. bicostata*)/Pink Gum (*E. fasciculosa*) woodland alliance.

cf. *Cacatua roseicapilla*

Material. incom. right ulna (178338), incom. left cmc. (167258).

Characters. These elements are of typical cacatuid form and are closest to those of *Cacatua roseicapilla* (see Baird, 1985).

Platycercidae

Platycercus elegans

Material. incom. rost. (1783), com. right hum. (167250), prox. end right hum. (167252), incom. left hum. (167247), com. right ulna (167256), com. right rad. (167260), incom. left ccd. (178570), huml. end right scap. (167261).

Characters. *Platycercus elegans* is the largest member of this genus in Victoria (Baird, 1985) and the fossil material agrees in mensural criteria to those of this species.

Remarks. *Platycercus elegans* "...is a bird of humid and semi-humid forests [ETOFF & EOFF], from sealevel to the highest mountains..." but "...post breeding flocks of immatures regularly come into open woodland [EWF], heathlands [HF] and partly cleared farmlands" (Forshaw, 1969). Currently recorded from EOFF and EWF in the south-east of South Australia (Parker & Reid, 1983).

Species previously unrecorded in the fossil record.

Neophema sp.

Material. incom. right ulna (167220), 1 incom. right fem. (178752).

Characters. These specimens could not be identified to species level since, for those elements, there is considerable overlap in size among the six species in the genus.

Psittaciformes

Family Indeterminate

Material. spinus proc. frag. (178507), incom. right fem. (178433).

Characters. Referred to the order Psittaciformes for being bifurcate (although not extreme) with little or no dorsal 'carina' on the spinus process (as in certain Passeriformes); the anterior section of the carina rounded; the whole *spinus proc.* largely dorsomedially extending.

Passeriformes

Hirundinidae

gen. et sp. indet.

Material. prox. end right hum. (167217), incom. left hum. (juv.) (167215), 2 incom. right ulna (178402, 178599), incom. left ulna (178408), incom. right tbt. (167235), dist. end left tbt. (juv.) (178446).

Characters. It is not considered possible to separate the various genera of Hirundinidae currently inhabiting continental Australia (see Baird, 1985).

Remarks. Presence of juvenile material suggests this species was nesting in the cave; therefore, it is regarded as autochthonous in origin.

Orthonychidae

Cinclosoma punctatum

Material. dist. end cran. (178370), right mand. art. (178377), com. right hum. (178387), com. left hum. (178511), incom. left ccd. (167243), com. right fem. (178438), com. left fem. (178423), dist. end right tmt. (178464), incom. left tmt. (juv.) (178457).

Characters. The postcranial elements of *C. punctatum* are larger than those of any other species in the genus *Cinclosoma*. All the abovementioned elements agreed in mensural criteria with comparable elements in a modern series of *C. punctatum* (see Baird, 1986).

Remarks. Most of the elements are completely ossified, except the proximal end of the tarsometatarsus (178457). I assume that they all came from the same individual and that, among the elements represented, the proximal end of the tarsometatarsus is the last to become fully ossified (based upon gross times of post

cranial bone ossification; see Latimer, 1927; Fujioka, 1955).

Cinclosoma punctatum occurs in most types of dry sclerophyll forest (EOFF: Frith, 1969; Morris *et al.*, 1981), and both Loyn (1985c) and Smith (1984) regard this species as occurring most frequently on dry ridges. Loyn (1980) describes its habitat as EOFF, "...specially where [the] understorey is sparse and there is a lot of plant litter, logs, and *Poa* spp."

Species previously unrecorded in the fossil record.

cf. *Cinclosoma punctatum*

Material. incom. stm. (juv.) (178346).

Characters. *Cinclosoma* can be identified by its proportionately anteriorly elongate *spina externa*, by its short more laterally projecting *proc. craniolateralis*, by the more arcuate nature of its *carina sterni* and its proportionately large *inc. lateralis*.

Acanthizidae

Dasyornis brachypterus

Material. 2 com. left hum. (178399, 167213), incom. left hum. (167163), prox. frag. left hum. (178401), com. right ulna (178409), com. left ulna (178407), 2 com. right fem. (178517, 178518), 4 com. left fem. (178427, 178428, 178431, 178602), 2 incom. left fem. (178429, 178430), com. right tbt. (167172), 4 incom. right tbt. (167171, 167231, 167232, 178448), prox. frag. right tbt. (178451), dist. end right tbt. (178449), incom. left tbt. (178528), 2 com. right tmt. (178463, 178613), 2 com. left tmt. (178453, 178454), dist. end left tmt. (178538).

Characters. *Dasyornis brachypterus* is intermediate in size between the other two species of *Dasyornis*. These mensural criteria are based on measurements from skins, the fossil material of *D. brachypterus* from Buchan, Victoria, and the fossil material of Western Bristlebird (*D. longirostris*) from the Cape Leeuwin/ Cape Naturaliste area of Western Australia (see Table 3). At present there are no modern comparative specimens of *D. brachypterus* and only one juvenile skeletal specimen of *D. longirostris*. The fossil material and the modern material fall into three distinct mensural groups (see Table 3); therefore, I am confident in the species-determination of this material as *D. brachypterus* (see Appendix VI and Fig.4).

Remarks. *Dasyornis brachypterus* is largely restricted to HF, especially that associated with watercourses, and rank vegetation, either bordering sub-coastal watercourses or along the coast (Morris *et al.*, 1981; Blakers *et al.*, 1984). McNamara (1946) in discussing the habitat preferences of *D. brachypterus* stated: "...it has been recorded from areas right on the seacoast and also from the tops of coastal ranges up to more than 2,000 feet above sealevel, there being a wide range in climatic conditions, though a high rainfall is common to both areas as is necessary to promote the growth of vegetation of the type they inhabit".

Species previously unrecorded in the fossil record. This is the only record for fossil *D. brachypterus* west of Buchan, Victoria, a range extension of approximately 780 km (see Fig.5; Baird, 1986).

Dasyornis broadbenti

Material. See Appendix IV.

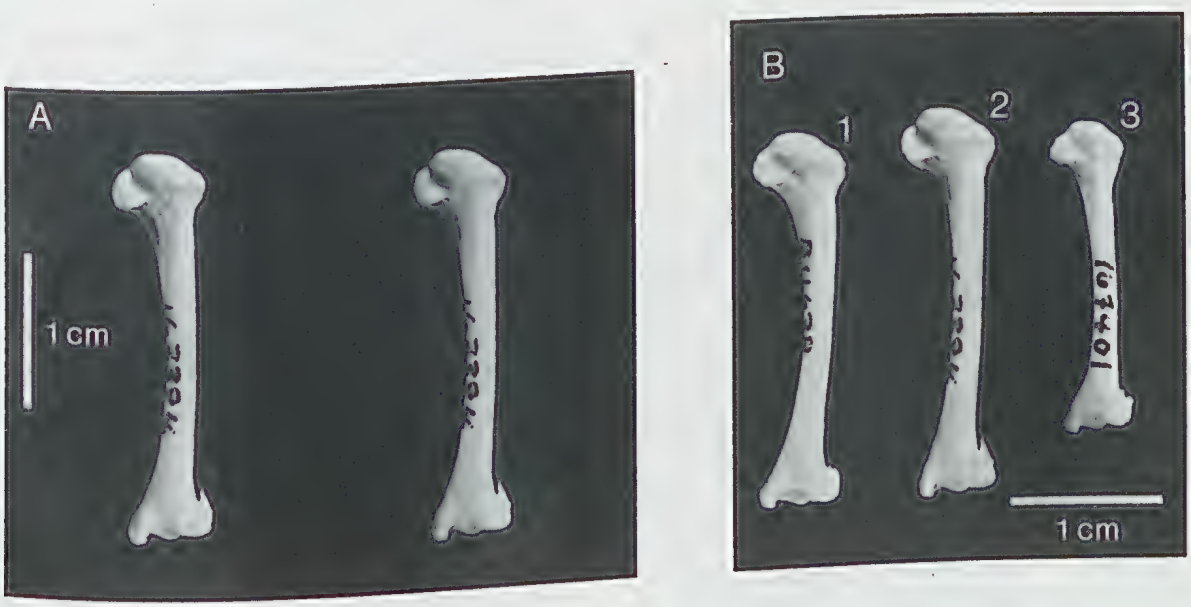

Fig.4. Stereo pair of a fossil right humerus (167394) referred to *Dasyornis broadbenti* (A), and a set of three right humeri (B) including (1) *Dasyornis broadbenti* (modern, MV B11638), (2) *D. broadbenti* (fossil from Amphitheatre Cave, 167394), and (3) *D. brachypterus* (fossil from Amphitheatre Cave, 167401).

Characters. Of the three species of *Dasyornis* in Australia, *D. broadbenti* is the largest. The referred fossil material is indistinguishable from comparable modern material of *D. broadbenti* (see Table 3 and Appendix VI).

Remarks. *Dasyornis broadbenti* is largely restricted to the coastal and subcoastal HF of the western coast of Victoria, but does occur in dense vegetation bordering streams in the Otway Ranges (see Fig.5; Blakers *et al.*, 1984).

Meliphagidae

cf. *Anthochaera carunculata*

Material. dist. end right hum. (167253), prox. end left hum. (178595), incom. right ccd. (167241), incom. left ccd. (167244), incom. right tbt. [juv.] (178533), incom. left tbt. (178478), incom. left tbt. [juv.] (178445), prox. end left tbt. [juv.] (167279), dist. end left tbt. [juv.] (167281).

Characters. Although morphological characters for the genera within the family Meliphagidae have not been worked out the material agrees in size with *Anthochaera carunculata*.

Remarks. *Anthochaera carunculata* "...lives...in eucalypt forest, woodland, mallee..." (Blakers *et al.*, 1985).

cf. *Anthochaera chrysoptera*

Material. incom. right ulna [juv.] (178513).

Characters. Although morphological characters for the genera within the family Meliphagidae have not been worked out the material agrees in size with *Anthochaera chrysoptera*.

Remarks. *Anthocharea chrysoptera* "...lives in eucalypt forest, heath and gardens mostly at low altitude in coastal and sub-coastal districts..." (Blakers *et al.*, 1985).

Paradiaseidae

Ptilonorhynchus violaceus

Material. left mand. art. (178378), com. right ulna (178339), incom. left ulna [juv.] (178340), incom. right ccd. (juv.) (178382), incom. left ccd. [juv.] (167242), incom. right fem. [juv.] (167266).

Characters. The fossil material conforms in all respects to those of modern comparative samples of the monotypic genus *P. violaceus*.

Remarks. *Ptilonorhynchus violaceus* ranges throughout a number of different habitats including EOFF, ETOFF and CFF, but its distribution seems to be centred on moist habitats including CFF and ETOFF (Morris *et al.*, 1981; Blakers *et al.*, 1984). The wide range of habitats comes from dispersal from summer breeding grounds during winter, for as Frith (1969) points out, "...locally it is abundant in the wet sclerophyll forests and moist gullies in the ranges and winter in the surrounding open country...".

Family previously unrecorded in the fossil record. This material constitutes a range extension of approximately 240 km west (Blakers *et al.*, 1984).

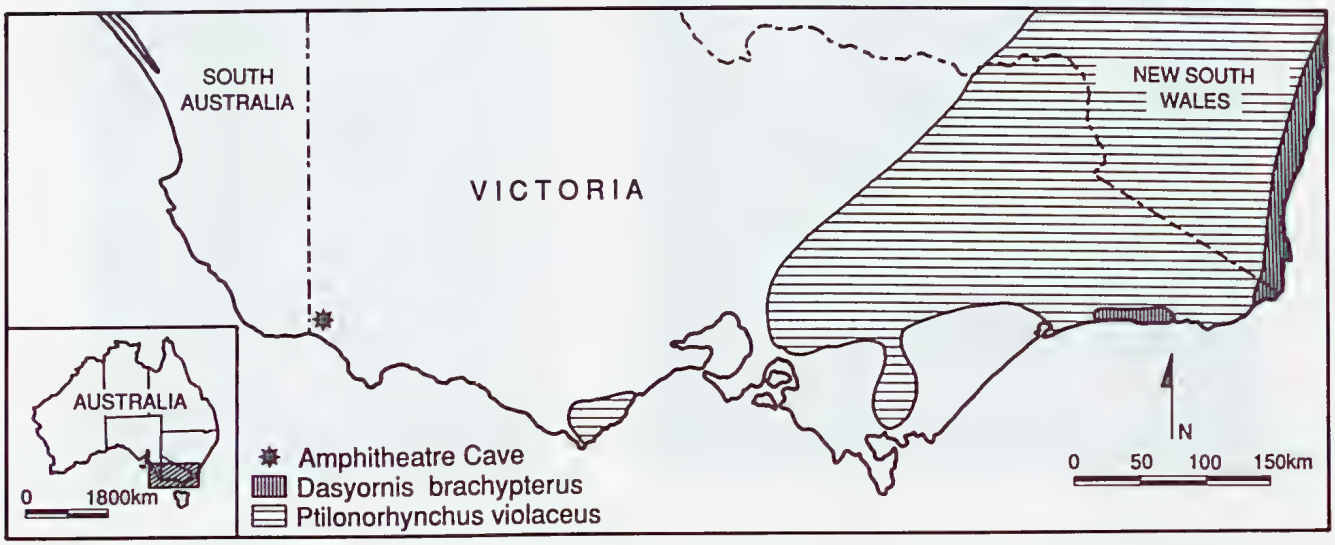

Fig.5. Distribution of *Dasyornis brachypterus* and *Ptilonorhynchus violaceus* in south-eastern Australia, including the fossil locality and current distributions.

Cracticidae

Indeterminate

Material. incom. right hum. (178660).

Characters. Species determination is not considered possible, for this element, because its length falls [L = 51.8] within the area of mensural overlap between *Gymnorhina tibicen* and *Strepera graculina*.

Corvidae

Corvus sp.

Material. prox. end right hum. (178343), dist. end right hum. (178342), incom. left cmc. (178659), incom. left tmt. (178341).

Characters. Species-determination not considered possible (see Baird, 1985).

Aves

Order Indeterminate

Material. huml. end left scap. (167184), incom. left fem. [juv.] (178527), shaft frag. right tbt. (178537), phal. dig. maj. (178516).

Passeriformes

Family Indeterminate

Material. 2 left ram. mand. (178376, 178588) spinus proc. frag. (178379), com. right ccd. (178466), stnl. end right ccd. (178383), com. left ccd. (178385), incom. left ccd. (178384), incom. right scap. (178380).

Fig.6. Stereoviews of *Ptilonorhynchus violaceus* femora, including (A) fossil specimen from Amphitheatre Cave (167266) and (B) modern specimen (MV W6490).

non-Passeriformes

Family Indeterminate

Material. incom. right ccd. [juv.] (178589), huml. end left scap. (178591).

Results and Discussion

The fossil avian assemblage from Amphitheatre Cave is composed of at least 27 species (MNI = 81), of which three species dominate the assemblage with 63% of the total MNI's (i.e., *Gallinula mortierii*, *Dasyornis brachypterus* and *D. broadbenti*; see Table 4). Out of these 27 species at least four are of questionable origin (see the Taphonomy section, below, for details).

Range extensions are noted for three species (i.e., *Gallinula mortierii*, *Dasyornis brachypterus* and *Ptilonorhynchus violaceus*), each of which is an indicator of a wetter climate than currently occurs in the area today (Fig.5).

Although previous dating of the deposit, based on faunal analysis, suggested a latest date of 12,000 y.B.P. by the presence of *G. mortierii* (Baird, 1984). A radiocarbon date of 4,670 ± 90 y.B.P. (NZA 700) has been obtained on a tibiotarsus identified as *Gallinula mortierii*. The date was made on the organic fraction of the bone (d13C: -23.42 per mille). Therefore *G. mortierii* is no longer considered reliable as an indicator of pre-Holocene deposits.

Taphonomy

Based on the condition of the elements, the avian assemblage from Amphitheatre Cave can be divided into two fractions. The first comprises bleached white elements with grains adhering to their surfaces and lack any carnivore damage. The second comprises elements whose coloration varies but is usually chamois (Munsell Notation, 1.7 Y 8.0/6.0; Smithe, 1975), whose surfaces are powdered with very minute gypsum crystals in the topographic depressions (J. Bodard, personal communication) and in many cases have very characteristic surficial weathering patterns. The taxa included in the first fraction are either pelagic or aquatic (i.e., *Eudyptula minor*, *Pachyptila* sp., *Phalacrocorax* sp., *Larus novaehollandiae*), and those in the second are largely terrestrial. I suggest that the material from the first fraction should not be included in a discussion of the taphonomic history of the cave assemblage, proper, for it is possible that it comprises beach washed specimens picked up either on the shore

line below the entrance of the cave by people who presumed them to have come from the cave itself, or at some undesignated point and included in the cave material by accident. The Glenelg River is tidal, at least to the Amphitheatre section, which would facilitate the transport of the pelagic species. The colouration, presence of sand grains, and habits of those members of this fraction would be compatible with such a scenario.

The material collected from the cave proper is characterised by the following: (i) it is composed of a wide variety (of which three predominate, numerically) of species, (ii) the range of body sizes for the species involved is great, with no centre of abundance at towards any end of the scale (see Fig.7), (iii) most (86%) of the individuals are terrestrial (see Fig.8), and (iv) elements are largely intact, with few acute or obtuse fractures (some right angle breaks are present). The hirundinid material was ignored in this analysis, as it is considered to be autochthonous/habitual cave-dweller in origin (see Baird, 1991a). The above-mentioned characters would be compatible with an autochthonous/pitfall/death trap origin for the bulk of the Amphitheatre Cave assemblage (Table 5; Baird, 1991a).

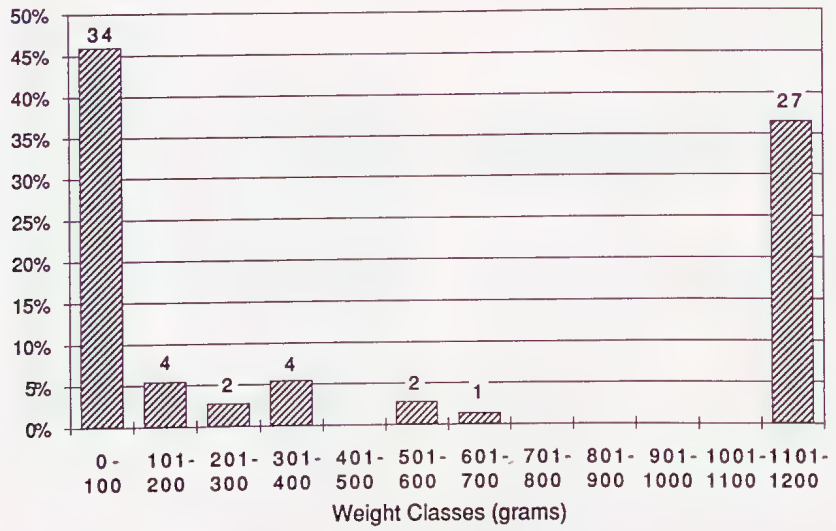

Fig.7. Percentage contribution of weight classes for bird species making up the Amphitheatre Cave avian assemblage showing no centre of distribution at either end of the weight scale. Numbers above the columns represent MNI from a total of 74. N = MNI from a total of 74. Not including *Eudyptula minor*, *Pachyptila* sp., *Phalacrocorax* sp., *Larus novaehollandiae* and Hirundinidae for reasons set out in the text.

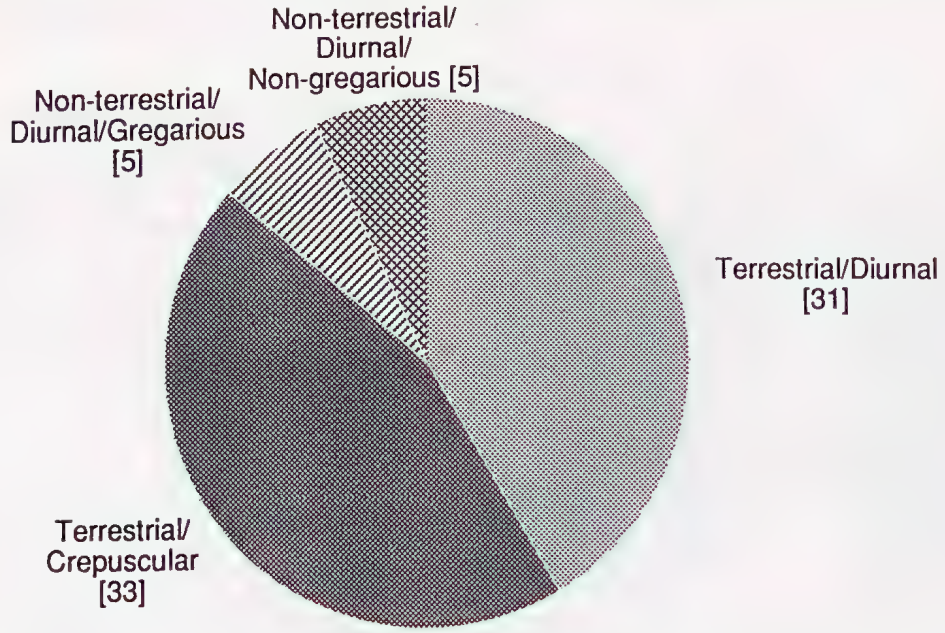

Fig.8. Percentages from total fauna (based on MNI = 74) of various avian behavioural groups from the Amphitheatre Cave avian assemblage demonstrating the large percentage of terrestrial individuals (figures in brackets are the MNIs for each group). Not including *Eudyptula minor*, *Pachyptila* sp., *Phalacrocorax* sp., *Larus novaehollandiae* and Hirundinidae for reasons set out in the text.

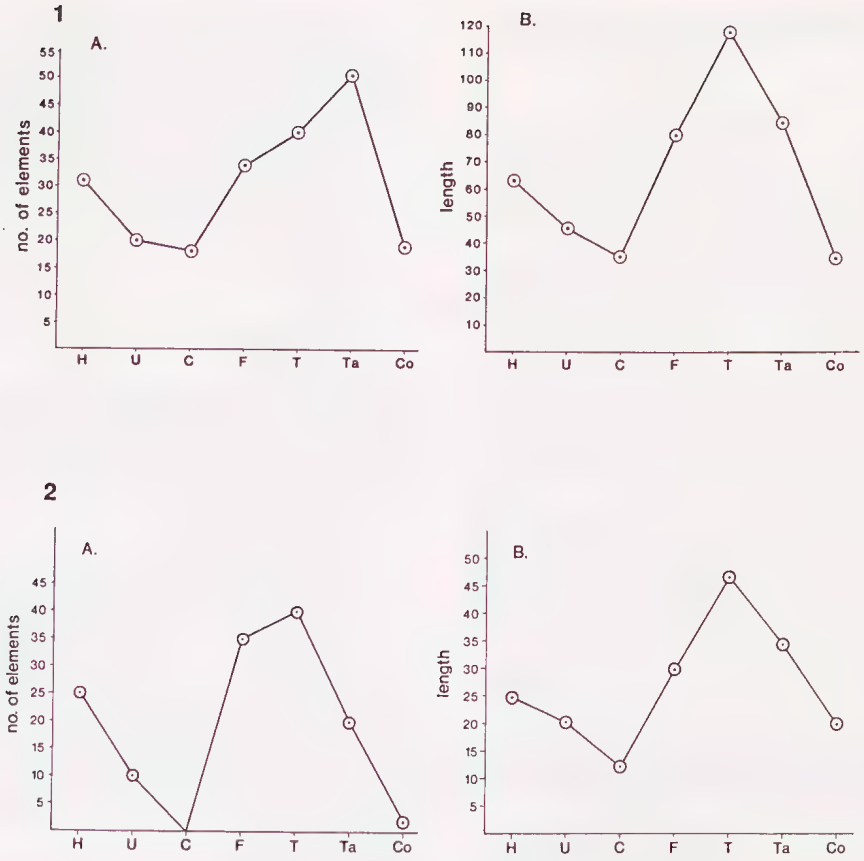

Fig.9. Graphic distribution of postcranial elements of *Gallinula mortierii* (Top) and *Dasyornis broadbenti* (Bottom) from Amphitheatre Cave demonstrating the bias for long bones by the collecting method of sieving with hands [A = element abundances and B = element total lengths]. H = humeri, U = ulnae, C = carpometacarpi, F = femora, T = tibiotarsi, Ta = tarsometatarsi and Co = coracoids.

Abundances of post-cranial elements are of no use in this case because the method of collection (i.e., through sieving with one's hands; Colliver, 1938) was biased towards long elements and against the short elements (see Fig.9).

Several species (e.g., *Cacatua tenuirostris*, *C. roseicapilla*, etc.) are of unknown taphonomic origin and may have been brought to the deposit from some distance by mammalian accumulators of bone, like the Tasmanian Devil [*Sarcophilus harrisii*] or Marsupial Wolf [*Thylacinus cynocephalus*], both of which occur in the deposit (Colliver, 1938).

Palaeoenvironmental Interpretation

Assuming that the assemblage from within the cave is contemporaneous, then it would be compatible with a reconstruction of the vegetation at the time of deposition that would have included; wetlands with some areas of short cropped grass, bordered by wet heathland, that subsequently gave way to EOFF away from the water source and ETOFF in the gullies (see Table 6). All of the vegetative formations would have been within the immediate area of the cave entrance at the time of deposition, because of the nature of the avian assemblage (i.e., autochthonous/pitfall; see Baird, 1991a).

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APPENDIX I

Table 1. Length measurements of the humeri [GL] for all of the *Turnix* spp. currently inhabiting south-eastern Australia demonstrating the affinities of the material from Amphitheatre Cave (G-2).

	μ	s-1	OR	N
T. varia	34.1	1.0	32.5 - 35.2	5
T. varia (G-2)	33.9	1.2	32.2 - 35.2	5
T. velox	24.6	1.3	23.3 - 26.7	5
T. pyrrhothorax	25.6	1.3	24.0 - 27.4	8

Table 2. Length measurements [La] of coracoids from the three species currently included in the genus *Phaps* demonstrating the affinities of the two specimens from Amphitheatre Cave (G-2).

	μ	s-1	OR	N
P. chalcoptera	34.6	1.1	33.0 - 36.0	10
P. chalcoptera (G-2)	34.0	-	-	1
P. histrionica	31.7	0.8	31.1 - 32.2	2
P. elegans	29.9	0.7	29.0 - 31.0	10
P. elegans (G-2)	30.8	-	-	1

Table 3. Greatest length of humeri [GL] for the three species of *Dasyornis*. Including samples from Mabel Cave (EB-1), Clogg's Cave (EB-2), Amphitheatre Cave (G-2), Skull Cave (AU-8), and Devil's Lair (WI-61E: see Rich & Baird, 1986) (unpublished data from Baird, 1986). M = modern comparative material.

		μ	s-1	OR	N
D. broadbenti	M	24.8	0.6	24.1 - 25.7	8
	G-2	25.5	0.8	24.3 - 27.0	22
D. brachypterus	EB-1	20.7	0.5	20.0 - 21.4	5
	EB-2	20.8	0.4	20.6 - 21.1	10
	G-2	20.6	0.8	19.8 - 21.5	4
D. longirostris	M	19.3	-	-	1
AU-8 + WI-61E		19.1	0.1	19.0 - 19.2	3

Table 4. List of avian species recorded in the deposits from Amphitheatre Cave (G-2).

	MNI	N
Spheniscidae		
Eudyptula minor	1	5
Procellariidae		
Pachyptila sp.	1	1
Phalacrocoracidae		
Phalacrocorax sp.	2	2
Anatidae		
small species	1	2
Accipitridae		
Accipiter fasciatus	1	1
Falconidae		
cf. *Falco cenchroides*	1	1
Phasianidae		
Coturnix sp.	2	14
Turnicidae		
Turnix varia	3	21
Rallidae		
Rallus philippensis	1	12
Gallinula mortierii	27	297
Laridae		
Larus novaehollandiae	1	1
Columbidae		
Phaps chalcoptera	1	1
P. elegans	1	1
Loriidae		
Glossopsitta concinna	1	2
Cacatuidae		
Cacatua tenuirostris	1	1
cf. *C. roseicapilla*	1	2
Platycercidae		
Platycercus elegans	1	8
Neophema sp.	1	2
Hirundinidae		
indeterminate	2	8
Orthonychidae		
Cinclosoma punctatum	1	9
cf. *Cinclosoma punctatum*	1	1
Acanthizidae		
Dasyornis brachypterus	6	27
D. broadbenti	18	88
Meliphagidae		
cf. *Anthochaera carunculata*	2	9
cf. *Anthochaera chrysoptera*	1	1
Paradisaeidae		
Ptilonorhynchus violaceus	1	6
Cracticidae		
Indeterminate	1	1
Corvidae		
Corvus sp.	1	4

Table 5. Avian taxa from excavations of Amphitheatre Cave and their proposed respective taphonomic accumulators (groupings).

Taphonomic group	Taphonomic agent	Species associated
Autochthonous	Pitfall/deathtrap	Anatidae small sp. *Coturnix* sp. *Turnix varia* *Rallus philippensis* *Gallinula mortierii* *Phaps chalcoptera* *P. elegans* *Cinclosoma punctatum* *Dasyornis brachypterus* *D. broadbenti* *Ptilonorhynchus violaceus* Cracticidae indet. *Corvus* sp.
Autochthonous/speleophiles	Natural Attrition	Hirundinidae indet.
Unknown	*Accipiter fasciatus*	cf. *Falco cenchroides* *Cacatua tenuirostris* *Glossopsitta concinna* *C. roseicapilla* *Platycercus elegans* cf. *Anthochaera carunculata* cf. *A. chrysoptera*

Table 6. Groups of taxa from the Amphitheatre Cave avian assemblage based on their usefulness in palaeoenvironmental interpretation (habitat specificity (exact/wide ranging) habitat distribution (patchy/regional)).

Wide ranging/Patchy	Wetlands	*Rallus philippensis* *Gallinula mortierii* Anatidae small sp.
	HF	*Phaps elegans* *Dasyornis broadbenti*
Wide ranging/Regional	EOFF	*Accipiter fasciatus* *Coturnix* sp. *Turnix varia* *Phaps chalcoptera* *Glossopsitta concinna* *Platycercus elegans* *Cinclosoma punctatum*
	EWF	*Cacatua tenuirostris* *C. roseicapilla*
Exact/Regional	Wet HF	*Dasyornis brachypterus*
	ETOFF	*Ptilonorhynchus violaceus*

APPENDIX II

List of abbreviations used in text, figures and appendices.

acet.	*acetabulum*
art.	*articularis*
a.p.s.l.	above present sea-level
ATSF	*Acacia* tall scrub formation
b.p.s.l.	below present sea level
cta	*crista*
ccd.	coracoid
CFF	Closed Forest Formation
cmc.	carpometacarpus
com.	complete
cond.	*condylus*
cot.	*cotyla*
cran.	cranium
dist.	distal
EOFF	*Eucalyptus* open forest formation
ETOFF	*Eucalyptus* tall open forest formation
EWF	*Eucalyptus* woodland formation
fac.	*facies*
fem.	femur
for.	*foramen/foramina*
frag.	fragment
furc.	furcula
HF	heathland formation
hum.	humerus
huml.	humeral
imp.	*impressio*
inc.	*incisura*
incom.	incomplete
juv.	juvenile
lig.	*ligamenta*
M.	*musculus*
mand.	mandible
M.N.I.	minimum number of individuals
MOSF	Mallee open scrub formation
N	number of elements in the statistical population
OR	observed range
osc.	*os coxae*
pel.	pelvis
proc.	*processus*
prox.	proximal
rad.	radius
ram.	*ramus*
rost.	rostrum
scap.	scapula
s	standard deviation
spin.	*spinus*
stm.	sternum
stnl.	sternal
sul.	*sulcus*
symph.	*symphysis*
syn.	synsacrum
tbt.	tibiotarsus
tmt.	tarsometatarsus
troc.	*trochlea*
tub.	*tuberculum*
μ	mean
y.B.P.	years Before Present

APPENDIX III

Suites of characters considered diagnostic for those taxa included in this study. Only those elements for which representatives occur in the cave deposit are included. The sequence of elements is standardised for ease of reference and includes the following: rostrum, cranium, mandible, humerus, ulna, carpometacarpus, coracoid, scapula, furcula, sternum, pelvis, synsacrum, femur, tibiotarsus and tarsometatarsus. For each of the long bones separate sections are provided for the proximal end, shaft and distal end (except for the coracoid which is divided into humeral end, shaft and sternal end) and each character is numbered. Not included in the analysis were the vertebrae, costal elements and phalanges.

SPHENISCIFORMES

Spheniscidae

The suites of characters considered diagnostic for the family Spheniscidae include: Synsacrum, (overall), 1. *cta ventralis* expanded ventrally (proximally), 2. short and stout: Femur, (proximal end), 1. *caput femori* projects proximomedially, 2. *fac. ventralis* excavated, 3. *cta trochanteris* merges gradually with shaft distally, 4. *fac. lateralis* flattened (with little topography); (shaft), 1. straight (not anteroposteriorly curved); (distal end), 1. laterally narrow, 2. *cond. medialis* and *cond. lateralis* pronounced dorsally, 3. *sul. patellaris* narrow: Tibiotarsus, (proximal end), 1. *cta cnemialis cranialis* short and stout, 2. *cta cnemialis* lateralis not expanded laterally and very stout, 3. *sul. interctalis* with numerous proximodistally running ridges; (shaft), 1. lateral edge rounded, 2. stout; (distal end), 1. offset from shaft to a small degree, 2. laterally flattened, 3. *inc. intercondylaris* shallow, 4. *cond. medialis* and *cond. lateralis* project distally an equal amount: Tarsometatarsus, (overall), 1. very laterally broad, 2. metatarsals incompletely fused.

ANSERIFORMES

Anatidae

The suites of characters considered diagnostic for the family Anatidae include: Coracoid, (humeral end), 1. axis of *proc. acrocoracoid* in line with that of shaft, 2. *cot. scapularis* large and deep, 3. *proc. procoracoid* broad and medially extending, 4. *sul. M. supracoracoidei* not bulbous or greatly expanded; (sternal end), 1. *imp. M. sternocoracoidei* very shallow, 2. *fac. art. sternalis* indistinct with a very faint bordering ridge (in dorsal view), 3. *fac. art. sternalis* only apparent along the mediosternal edge (in ventral view); Tibiotarsus, (proximal end), 1. *cta cnemialis cranialis* not markedly expanded proximally, 2. *cta cnemialis lateralis* markedly expanded laterally; (shaft), 1. ventral surface flattened, adjacent to *cta fibularis*; (distal end), 1. offset laterally, 2. *sul. extensorius* centered on shaft, 3. *cond. lateralis* extends further distally than *cond. medialis*.

GALLIFORMES

Phasianidae

Coturnix: The following suites of characters are considered diagnostic for the genus *Coturnix*: Rostrum, 1. anteroposteriorly short, 2. *os premaxilla* broad and rounded anteriorly (viewed dorsally), 3. nasal opercula anteroposteriorly short and rounded on all sides, 4. os nasale dorsal arm gracile; Humerus, (proximal end), 1. double *fossa pneumotricipitalis*, distinctly separated by *margo caudalis* (not *crus dorsale fossa* as in passerines), 2. *caput humeri* with small dome, 3. *cta pectoralis* with very small apical overhanging prominence; (shaft), 1. shaft laterally flattened; (distal end), 1. *fossa M. brachialis* relatively small and posteriorly projecting, 2. *cond. dorsalis* anteroposteriorly aligned, 3. *cond. ventralis* with angular posterior margin, 4. *proc. supracondylaris dorsalis* very small and rounded: Ulna, (proximal end), 1. olecranon acute proximally and dorsoventrally flattened, 2. *tub. lig. collateralis ventralis* not prominent, 3. dorsal margin of *cot. dorsalis* rounded; (shaft), 1. dorsoventrally flattened (width greater than depth): Coracoid, (humeral end), 1. *proc. procoracoid* very reduced; (shaft and sternal end), 1. *imp. M. sternocoracoidei* shallow and limited to sternal end, 2. *proc. lateralis* pronounced but relatively small: Tarsometatarsus, (proximal end), 1. medial *fora. vascularia proximalia* further proximal than lateral *fora. vascularia proximalia*, 2. a single tendinal canal along medial side of *hypotarsus*, 3. one major open *sul. hypotarsi*, 4. base of *hypotarsus* excavated; (distal end), 1. ventral extension of *troc. metatarsi II* rounded and solid, 2. *fossa metatarsi I* present.

GRUIFORMES

Turnicidae

Turnix. The following suites of characters are considered diagnostic for the genus *Turnix*: Humerus, (proximal end), 1. single large *fossa pneumotricipitalis*, 2. deep, proximodistally elongate groove on palmar face of *tub. dorsale*, 3. *caput humeri* highly domed, 4. *cta pectoralis* with large tuberosity, 5. *tub.* present of proximal-most point of *margo caudalis*; (distal end), 1. *fossa M. brachialis* relatively large and anteriorly projecting, 2. main axis of *cond. dorsalis* laterally aligned, 3. *cond. ventralis* with rounded posterior margin, 4. *proc.* supracondylaris dorsalis relatively large and distally acute: Ulna; (proximal end), 1. *olecranon* acute proximally and not laterally flattened, 2. *tub. lig. collateralis* ventralis forms a prominent shelf, 3. dorsal margin of *cot. dorsalis* angular; (shaft), 1. not dorsoventrally flattened (width and depth subequal): Carpometacarpus, (proximal end), 1. *cta dorsalis* of *troc. carpalis* extends distally, 2. *cta ventralis* of *troc. carpalis* with an even, rounded margin, 3. *proc. piciformis* acute distally; (shaft), 1. *os metacarpus majus* with no *proc. intermetacarpale*, 2. *os metacarpus minus* with a smooth distal margin: Coracoid, (humeral end), 1. *proc. procoracoid* closes on *fac. art. clavicularis* of *proc. acrocoracoid* forming a definite canal between them, 2. whole coracohumeral surface well developed and nearly at right angles to shaft, humerally; (shaft and distal end), 1. *imp. M. sternocoracoidei* deep and humerosternally extensive, 2. *proc. lateralis* pronounced: Sternum, 1. *carina sterni* anteriorly projecting and deep: Femur, (proximal end), 1. *cta trochanteris* extends distally very briefly, 2. one prominent muscular insertion proximally

and one very small muscular insertion distally, 3. distal muscular insertion is the continuation of *linea intermuscularis caudalis*; (distal end), 1. *cond. medialis* slopes gradually to shaft, proximally, 2. *imp. ansae M. iliofibularis* in contact with *troc. fibularis* but also extends proximally: Tibiotarsus, (proximal end), 1. *caput tibiotarsi* not laterally compressed, 2. *cta cnemialis* lateralis extends laterally and points distally but does so gradual manner, 3. *cta cnemialis cranialis* large; (shaft), 1. *cta fibularis* markedly delineated on both proximal and distal ends, and does not approach *cta cnemialis lateralis*, 2. shaft not dorsoventrally flattened; (distal end), 1. *inc. intercondylaris* small, 2. *cond. medialis* distally foreshortened with a pronounced lateral extension on dorsal lip: Tarsometatarsus, (proximal end), 1. medial *fora. vascularia proximalia* further distal than lateral *fora. vascularia proximalia*, 2. single tendinal canal almost centred in *hypotarsus*, 3. two nearly closed *sulci hypotarsi*, 4. base of *hypotarsus* swollen; (distal end), 1. ventral extension of *troc. metatarsi II* anteroposteriorly elongate and laterally flattened, 2. no *fossa metatarsi I*.

Rallidae

Rallinae

The following suite of characters are considered diagnostic for the subfamily Rallinae: Rostrum, 1. anteroposteriorly elongate, 2. nasal operculum anteroposteriorly elongate and rounded on all sides, 3. *os nasale* dorsal arm robust: Humerus, (proximal end), 1. main axis of *inc. capitis* approaches that of shaft, 2. single *fossa pneumotricipitalis*, 3. main axis of *caput humeri* parallel to that of *inc. capitis*; (distal end), 1. *proc. supracondylaris* dorsalis small and rounded, 2. distal end narrow, 3. *proc. flexorius* extends as far or farther than *cond. ventralis*: Ulna, (proximal end), 1. *sul. M. brachialis* small, 2. *cot. ventralis* completely enclosed, 3. *cot. ventralis* does not extend upon *olecranon*: Radius, (shaft), 1. *corpus radii* short, straight and stout; (distal end), 1. *sul. ligimenta* shallow: Carpometacarpus, (proximal end), 1. *proc. extensorius* tends proximolaterally, 2. *troc. carpalis* extends proximally and acute at its proximal most point, 3. *os metacarpus minus* and *majus* subparallel: Sternum, 1. single notched, 2. *rostrum sterni* small: Pelvis, 1. laterally flattened, 2. *cta iliaca dorsalis* fuse to *cta dorsalis* of synsacrum, proximally, 3. *tub. preacetabulare* pronounced, 4. pelvis deep in lateral view, 5. strong *cta iliaca dorsolateralis*: Coracoid, (proximal end), 1. *proc. procoracoid* pronounced and extends further medially than *proc. acrocoracoid*, 2. *cot. scapularis* large and deep, 3. *fac. art. humeralis* flares strongly laterally; (distally), 1. *imp. M. sternocoracoidius* deep: Femur, (proximal end), 1. *cta trochanteris* extends dorsally not proximally, 2. *sul. M. iliotrochantericus caudalis* restricted to extreme proximal end of *trochanter*; (shaft), 1. pronounced curve, (in lateral view), 2.strong ridge extending from ventral portion of *cta trochanteris* distally, and in some case extends to distal end: Tibiotarsus, (proximal end), 1. proximodistally flattened *cta cnemialis lateralis*; (shaft), 1. broad, flat area adjacent to *cta fibularis*, viewed ventrally; (distal end), 1. area below *sul. extensorius* expanded distally, increasing depth of *inc. intercondylaris*, 2. *fac. lateralis* of epicondyle lateralis rounded: Tarsometatarsus, (proximal end), 1. *caput carpalis* tapers gradually to shaft, distally (in dorsal view), 2. *cta lateralis hypotarsi* extended distally; (shaft), 1. dorsal surface flat (not concave); (distal end), 1. *troc. metatarsi III* strongly rotated positioned almost completely below shaft.

PSITTACIFORMES

The following suite of characters are considered diagnostic for the order Psittaciformes: Humerus, (proximal end), 1. *imp. M. coracobrachialis cranialis* prominent, 2. tub. dorsale deeply excavated and restricted, distally, to medial edge of *tub. ventrale*, 3. whole prox. head rotated counterclockwise (in distal view); (distal end), 1. *cond. ventralis* not prominent and extends distally as much as *proc. flexorius*, 2. *proc. supracondylaris dorsalis* insignificant and distal (i.e., closer to *epicondylus dorsalis*): Ulna, (proximal end), 1. lateral edge of *cot. ventralis* nearly round (viewed proximally), 2. *olecranon* short and blunt, 3. *tub. lig. collateralis ventralis* with little lateral extension; (shaft), 1. *papillae remigiales caudales* insignificant, 2. shaft width and depth subequal, 3. shaft curved; (distal end), 1. laterally flared, 2. *cond. ventralis* prominent and extends furthest distally, 3. *sul. radialis* deep with distinct borders: Radius, (shaft), 1. *corpus radii* stout,long and curved; (distal end), 1. *sul. ligimenta* not present, 2. *tub. aponeurosus* large, rounded and distally extending, 3. tub. on *facies ventralis* prominent and rounded: Carpometacarpus, (proximal end), 1. *proc. extensorius* elongate and tends laterally; (shaft and distal end), 1. no *proc.* intermetacarpalis (or insignificant), 2. ventral ridges of *os metacarpale majus* and *minus* extend to just distal to *proc. pisiformis* (in palmar view): Coracoid, (humeral end), 1. *proc. acrocoracoid.* extends and tapers to meld with *fac. art. humeralis*, 2. distance between *proc. acrocoracoid.* and *cot. scapul.* narrow, 3. *cot. scapularis* narrow and restricted to *proc. cot. scapularis*, 4. presence of pneumatic fenestrae at interface of *sul. M. supracoracoidei* and *fac. art. clavicularis*; (sternal end), 1. *angularis medialis* narrowly attaches to main body of coracoid, 2. *proc. lateralis* does not extend beyond lateral most extension of *fac. art. sternalis*: Femur, (proximal end), 1. *trochanter* with no proximal extension, 2. *cta trochanteris* rounded, stout and restricted to dorsal surface, 3. *cta obturator* produced not by ventral extension of *trochanter* but by presence of two large fossa just distal to *trochanter*, 4. *caput femoralis* relatively large with a stout neck; (shaft), 1. straight; (distal end), 1. *cond. medialis* expanded proximodistally.

Loriidae

Elements referred to the family Loriidae are based on the following characters: Ulna, (shaft), 1. stout, 2. large curvature; (whole), 1. medium to small size (this suite of characters also present in *Lathamus*); Carpometacarpus, 1. *os metacarpus majus* stout, 2. *proc. extensorius* anteriorly elongate, 3. *proc. extensorius* at greater angle to shaft, viewed laterally, 4. *proc. pisiformis* located further distally.

Glossopsitta

Elements are referred to the genus *Glossopsitta*, for the presence of the following suites of characters, including: Ulna, based upon mensural characters; Carpometacarpus, (proximal end), 1. facet for insertion of *lig. radiocarpometacarpale* more lateral on *troc. carpalis*, 2. more distally located *proc. pisiformis*, 3. T.L. less than 20 mm.

Platycercidae

Elements are referred to the family Platycercidae based on

the following characters: Humerus, (proximal end), 1. faint broad second *fossa pneumotricipitalis*, 2. narrow based *caput humeri*, 3. distal extension of *caput humeri* on palmar face, 4. *cta bicipitalis* expanded laterodistally and abruptly attaches to shaft distally (except in Pezoporinae): Ulna, (shaft), 1. shallow curvature, 2. gracile; (whole), 1. medium size (this suite of elements does not cover small *Psephotus* spp. and all *Neophema* spp.): Coracoid, (humeral end), 1. *proc. acrocoracoid* bulbous; (sternal end), 1. narrow *fac. art. lateralis*, 2. *proc. lateralis* attenuate laterally, 3. *imp. M. sternocoracoidei* deep: Femur, (proximal end), 1. *cta trochanteris* surpasses *caput femora* proximally.

Platycercus

Elements are referred to the genus *Platycercus* based on the following characters: Rostrum, 1. curved moderately, 2. external nares located further distally on rostrum, 3. *culmen* rounded laterally: Humerus, as for family: Ulna, as for family: Carpometacarpus; (proximal end), 1. facet for insertion of unknown lig. interrupts *cta dorsalis* of *troc. carpalis*, 2. *spatium intermetacarpale* of medium width, 3. *proc. extensorius* projects proximomedially, 4. not laterally narrow or broad, 5. head proximodistally shortened, 6. mensural characters, intermediate in size: Coracoid, (humeral end), 1. *proc. acrocoracoideus* rounded humerally, 2. *tub.* on internal face of *proc. acrocoracoid* not markedly raised above adjacent areas, 3. sternal end narrower than in *Barnardius* but identical to *Purpureicephalus*, 4. T.L. greater than 10 mm.

Neophema

Elements are referred to the genus *Neophema* based on the following characters: Ulna, (shaft), 1. moderate curvature, 2. gracile; (whole), 1. small elements (this suite of characters also pertains to small spp. of *Psephotus*); Femur, (whole), 1. very long and gracile; (distal end), 1. *cta dorsalis* of *cond. medialis* larger and more prominent than that of *cond. lateralis*, 2. very narrow, 3. twisted distolaterally (the same suite of characters can be seen in *Pezoporus* but are less pronounced in *Neophema*)

PASSERIFORMES

Hirundinidae

gen. et sp. indet.

Gen. et sp. indeterminate. Elements are referred to the family Hirundinidae based on the following characters: Humerus, (proximal end), 1. very strongly developed proximal edge of *cta pectoralis*, 2. shelf created by palmar expansion of *caput humeri* and proximal edge of *cta pectoralis*, 3. *cta pectoralis* well developed with palmar face concave, 4. single *fossa pneumotricipitalis*; (distal end), 1. long (lateral) axis of distal end rotated approximately 45 degrees from long (lateral) axis of proximal end, 2. well developed *proc. supracondylaris* dorsalis, 3. *cond. dorsalis* expanded distally, 4. *fossa M. brachialis* shallow: Ulna, (proximal end), 1. *cotyla dorsalis* proximodistally elongate, 2. *tub. lig. collateralis ventralis* prominent, 3. *olecranon* laterally compressed; (shaft), 1. short, stout and straight: Tibiotarsus, (distal end), 1. condyles positioned distally to the distal opening of the *canalis extensorius*.

Orthonychidae

Cinclosoma

Cinclosoma. Elements are referred to the genus *Cinclosoma* for the presence of the following characters: Humerus, (proximal end), 1. *crus dorsale fossa* very stout and extends past *tub. dorsale*, 2. *caput humeri* broad and flat with a prominence just proximal to *margo caudalis*, 3. *cta pectoralis* proximodistally short (not extending past *cta bicipitalis* distally) and ventrally swollen; (shaft) 1. stout; (distal end) 1. *proc. flexorius* broad and highly sculpted: Coracoid, (humeral end), 1. *proc. acrocoracoideus* laterally compressed, 2. *fac. art. clavicularis* with deep fossa: Femur, (proximal end), 1. no *fossa trochanteris*, 2. *cta trochanteris* not extended proximally, only weakly extended dorsally and junction of two sections forms a sharp point, 3. *cta ventralis* of *caput femoris* present with no excavation of *fac. ventralis*, 4. no distal extension of *cta trochanteris*, 5. *tub. M. iliofemoralis externus* and *tub. M. iliotrochanteris caudalis* concentrated on dorsoventral portion of *fac. lateralis*, 6. *tub. M. iliotrochanteris caudalis* angles abruptly distally, 7. *tub. M. ischiofemoralis* very small and proximodistally short; (shaft), 1. stout: Tarsometatarsus, (distally), 1. shaft gradually expands laterally to *troc. metatarsi* (smooth continuous curve), 2. all *troc. metatarsi* in same lateral plane, 3. *for. vasculare distale* minute or non-existent, 4. *troc. metatarsi II* laterally expanded with a very shallow sulcus, 5. *troc. metatarsi III* with definite but shallow sulcus, 6. *troc. metatarsi IV* laterally expanded but with no sulcus, 7. *inc. intertrochlearis* very shallow (anteroposteriorly).

Acanthizidae

Dasyornis

Dasyornis. Elements are referred to the genus *Dasyornis* based on the following characters: Humerus, (proximal end), see Baird, 1985: Ulna, (overall), markedly short and stout, and agrees in size with *Dasyornis*: Femur, (proximal end), 1. *cta trochanteris* expanded dorsally, not proximally, 2. *cta trochanteris* extends distally, 3. *fossa trochanteris* present along whole length of *cta trochanteris*, 4. *tub. M. iliotrochantericus cranialis* small and centrally located on *fac. lateralis*, 5. *fac. art. antitrochanteris* broad dorsally (in proximal view), 6. *fac. ventralis* excavated; (shaft), 1. markedly curved ventrally, distal to midpoint of shaft, 2. laterally flattened; (distal end), 1. *imp. ansae M. iliofibularis* pronounced, 2. *imp. ansae M. iliofibularis* not joined to *cta tibiofibularis lateralis*, 3. *epicondylus medialis* excavated and proximodistally elongate, 4. medioventral edge of *cond. medialis* expanded proximally: Tibiotarsus, (see Baird, 1985): Tarsometatarsus, (distal end), 1. all troc. metatarsi on distinct slope medially off of shaft axis, 2. lateral edge of *troc. metatarsi* IV expanded (over inner edge) and narrow, 3. medial edge of *troc. metatarsi* II very narrow with a definite shelf laterally.

Meliphagidae

The suite of characters considered diagnostic for the family Meliphagidae include: Humerus, (proximal end), 1. *cta bicipitalis* concave proximally, 2. single *fossa pneumotricipitalis*, 3. *cta pectoralis* extends past junction of *cta bicipitalis* and shaft,

distally, 4. *crus ventrale* fossa extends past *tub. ventrale* ventrally (in palmar aspect), 5. *cta pectoralis* ends abruptly distally, 6. *inc. capitis* proximodistally narrow and deep: Coracoid, (proximal end), 1. *proc. acrocoracoideus* laterally broad, 2. *fac. art. clavicularis* with deep fossa (similar to the Cracticidae): Tibiotarsus, (proximal end), 1. *cta cnemialis* lateralis expanded laterally, 2. *sulcus intercristalis* deep, 3. *tub. M. femorotibialis* interior distinct, 4. area between *tub. M. femorotibialis interior* and proximal-most point on *cta cnemialis cranialis* depressed; (shaft), 1. anteromedial edge of shaft expanded medially, viewed ventrally; (distal end), 1. laterally wide, 2. proximodistally elongate, 3. *inc. lig. intercondylaris* proximodistally elongate, 4. *pons supratendinosus* proximodistally elongate, 5. *cta intercondylaris* present in *sulcus cartilaginus tibialis.*

Paradisaeidae

Ptilonorhynchus and *Ailuroedus*

Ptilonorhynchus and *Ailuroedus*. The suite of characters considered diagnostic for the genera *Ptilonorhynchus* and *Ailuroedus* include; Ulna, (proximal end), 1. *olecranon* pointed proximally and not angles back so as to point more laterally, 2. dorsal surface of *cot. dorsalis* flattened, in proximal view, 3. *cot. dorsalis* proximodistally elongate: Coracoid, (humeral end), 1. *proc. acrocoracoid* not tilted medially, 2. *proc. acrocoracoideus* anteriorly extending and acute, 3. *sul. M. supracoracoidei* shallow, 4. *proc. procoracoideus* prominent, 5. *proc. acrocoracoideus* bulbous along its most humeral edge (ventral view); (distal end), 1. *proc. lateralis* with strong laterally tending *proc.* at its humeral most point, 2. *fac. art. sternalis* laterally broad: Femur, (proximal end), 1. long axis of *tub. M. iliotrochanteris caudalis* proximodistally aligned, 2. *tub. M. iliofemoralis externus* and *tub. iliotrochanteris caudalis* not attached or continuous, 3. *tub. M. ischiofemoralis* very proximodistally elongate and central on *fac. lateralis*, 4. *tub. M. iliotrochanteris cranialis* separate from *tub. M. ischiofemoralis* but forms part of main body of *cta trochanteris.*

Cractidae

The suite of characters considered diagnostic for the family Cracticidae include: Humerus (proximal end), 1. single *fossa pneumotricipitalis*, 2. cta *bicipitalis* convex distally, 3. *tub. ventrale* relatively small and elevated portion laterally restricted, 4. *cta pectoralis* does not extend as far down shaft distally, 5. *crus dorsale fossae* projects anconally, 6. *cta pectoralis* ends abruptly distally, 7. *tub. M. scapulohumeralis* anterior distinct, 8. transition from *caput humeri* to *cta pectoralis* smooth; (shaft), 1. smooth arc to ventral edge as far as *proc. flexorius* (in palmar view); (distal end), 1. *proc. flexorius* extends distolaterally.

Corvidae

The suite of characters considered diagnostic for the family Corvidae include: Humerus, (proximal end), 1. *crus dorsale fossa* projects distally to shaft, 2. *cta pectoralis* long and melds with shaft distally, 3. *cta bicipitalis* concave proximally, 4. tub. ventrale large and elevated portion not laterally restricted, 5. *tub. M. scapulohumeralis anterior* indistinct but has a distinct ridge extending distally from its base, 6. transition from *caput humeri* to *cta pectoralis* smooth, 7. single *fossa pneumotricipitalis;* (shaft), 1. smooth arc to ventral edge as far as *proc. flexorius* (in palmar view); (distal end), 1. *proc. flexorius* extends distolaterally: Carpometacarpus, 1. mensural characters, larger than all other Australian passerines: Tarsometatarsus, (overall), 1. TL greater than 45; (shaft), 1. mediodistal edge smooth and continuous to distal end (not broken by reinforcement for *fossa metatarsi I*); (distal end), 1. inc. intertrochlearis narrow proximally, 2. *troc. metatarsi II* expanded laterally, 3. *troc. metatarsi II* and *IV* lack sulci, 4. proximal edge of *troc. metatarsi IV* does extend as far proximally as that of *troc. metatarsi III*, 5. lateral and medial edges of *troc. metatarsi IV* parallel, 6. *cta medialis* of *troc. metatarsi III* only slightly expanded, distally and dorsally, over *cta lateralis*, 7. *troc. metatarsi III* and *IV* relatively broad, laterally.

APPENDIX IV

Rallidae

Gallinula mortierii

Material. 4 incom. cran. (167104-167106, 178345), incom. rost. (178749), 2 incom. rost. (178348, 178542), com. mand. (178750), 5 right ram. mand. (178350-178353, 178543), 2 left ram. mand. (178499, 178544), 2 dist. symph. mand. (167107, 178349), 8 com. right hum. (167005-167008, 167086-167088, 167124), 2 incom. right hum. (167125, 167126), 2 prox. end right hum. (178355, 178553), 9 com. left hum. (167001, 167004, 167061, 167084, 167085, 178477, 178551, 178620, 178621), 7 incom. left hum. (167002, 167003, 167118-167121, 178315), incom. left hum (juv.) (167038), 3 prox. end left hum. (167122, 178314, 178552), 2 dist. end left hum. (167037, 167123), 7 com. right ulna (167062, 167063, 167127, 167128, 167195, 178356, 178558), 3 incom. right ulna (167129, 167130, 178559), prox. end right ulna (167196), dist. end right ulna (178560), 4 com. left ulna (167191, 178316, 178554, 178557), 4 incom. left ulna (167192, 167193, 178555, 178556), incom. left ulna (juv.) (167254), prox. end left ulna (167194), com. right rad. (178357), 5 incom. right rad. (167131, 167197, 167198, 167259, 178563), 2 com. left rad. (178561, 178562), 5 com. right cmc. (167201, 178317, 178318, 178359, 178584), 3 incom. right cmc. (167202, 178319, 178358), incom. right cmc. (juv.) (178360), 6 com. left cmc. (167132, 167134, 167199, 167200, 178503, 178586), 3 incom. left cmc. (167133, 178585, 178622), 3 incom. stm. (167307, 178474, 178475), 3 stm. frag. (167116, 167117, 167181), 4 com. right scap. (167050, 167114, 178547, 178548), 4 incom. right scap. (167113 167115, 167190, 178546), 3 com. left scap. (178313, 178500, 178549), 3 incom. left scap. (167059, 178312, 178501), incom. left scap. (juv.) (167058), 8 com. right ccd. (167187-167189, 167308, 167309, 178310, 178476, 178545), 3 incom. right ccd. (167109-167111), 2 incom. right ccd. (juv.) (178337, 178589), huml.

end right ccd. (167112), 2 com. left ccd. (167056, 167057), 3 incom. left ccd. (167186, 178311, 178354), huml. end left ccd. (167108), 10 incom. pel. (167064, 167135, 167136, 167203, 167204, 178467-178471, 178478, 178623, 178624), 3 prox. end pel. (167135, 167136, 178471), 3 incom. syn. (178479, 178481, 178626), 3 prox. end syn (178473, 178497, 178627), 3 dist. end syn. (167065, 178344, 178480), 2 left os pelvis (178564, 178565), left os pelvis (juv.) (178472), 3 right acet. frag. (167138, 167139, 178361), 3 left acet. frag. (167137, 167140, 178566), 4 com. right fem. (178630, 178631, 178633, 178634), 8 incom. right fem. (#, 167013-167015, 167143, 167144, 178629, 178632), incom. right fem. (juv.) (178635), dist. end right fem. (167016), 4 com. left fem. (167010, 167090, 178637, 178638), 13 incom. left fem. (167011, 167012, 167040, 167041, 167066, 167089, 167091, 167092, 167141, 178482, 178567, 178636, 178639), 3 incom. left fem (juv.) (167009, 167039, 167142), prox. end left fem. (167093), 2 com. right tbt. (167098, 178486), 8 incom. right tbt. (167034, 167035, 167096, 167097, 167148, 178484, 178485, 178570), 2 incom. right tbt. (juv.) (167036, 178483), 2 prox. end right tbt. (167019, 167020), dist. end right tbt. (167147), dist. end right tbt. (juv.) (167021), 7 com. left tbt. (167026, 167028, 167029, 167145, 178488, 178568, 178644), 10 incom. left tbt. (167027, 167030, 167094, 167146, 178487, 178489, 178640-178643), 2 incom. left tbt. (juv.) (167032, 167033), 3 prox. end left tbt. (178748, 167160, 178490), 6 dist. end left tbt. (167017, 167018, 167031, 167095, 178569, 178645), dist. end left tbt. (juv.) (178320), 11 com. right tmt. (167048-167052, 167100, 167101, 178493, 178494, 178653-178655), 10 incom. right tmt. (167025, 167024, 167049, 167100, 167101, 167155, 167158, 178495, 178574), 2 incom. right tmt. (juv.) (167053, 178656), 2 dist. end right tmt. (juv.) (178322, 178324), 12 com. left tmt. (167022, 167023, 167044, 167149, 167150, 178491, 178496, 178646, 178648-178651), 8 incom. left tmt. (167042, 167043, 167099, 167151, 167152, 167156, 178647, 178652), 2 incom. left tmt. (juv.) (167046, 167153), 3 dist. end left tmt. (167045, 167067, 167154), dist. end left tmt. (juv.) (167047), 30 unspecified phalanges (167159, 167239, 167301-167306, 178325-178335, 178347, 178575-178583, 178587).

Acanthizidae

Dasyornis broadbenti

Material. incom. mand. (178372), dist. mand. symph. (178505), 2 right ram. mand. (167205, 167206), 4 left ram. mand. (178373-178375, 178506), 9 com. right hum. (167164, 167216, 167249, 178394-178397, 178596, 178598), 2 incom. right hum. (178398, 178597), dist. end right hum. (167165), 8 com. left hum. (167161, 167162, 167212, 167218, 178388, 178389, 178512, 178594), 3 incom. left hum. (167245, 178392, 178593), 2 prox. end left hum. (178390, 178391), prox. shaft frag. left hum. (178393), dist. end left hum. (167214), 6 com. right ulna (167221, 178403-178405, 178515, 178600), 3 com. left ulna (167226, 167227, 178406), incom. left ulna (178406), 2 incom. right ccd. (167211, 178510), 1 incom. stm. (167072), 3 incom. pel. (178411, 178412, 178415), 5 com. syn. (167073, 178410, 178413, 178414, 178416), 2 incom. syn. (178417, 178418), 3 pel. frag. (178419-178420), 13 com. right fem. (167075, 167168, 167169, 167267-167269, 178436-178439, 178519-178521, 178604), 4 incom. right fem. (167185, 167270, 178434, 178435), shaft frag. right fem. (178440), dist. frag. right fem. (167170), 10 com. left fem. (167166, 167262, 167264, 178422, 178424-178426, 178523-178525), 6 incom. left fem. (167076, 167263, 178432, 178522, 178603, 178751), prox. end left fem. (178526), dist. end left fem. (167265), com. right tbt. (178531), 12 incom. right tbt. (167077, 167078, 167173, 167175, 167176, 167282-167284, 167287, 178447, 178532, 178534), 5 prox. end right tbt. (167285, 167286, 167288, 167289, 178536), 2 shaft frag. right tbt. (167082, 178535), 4 dist. end right tbt. (167174, 167290, 178450, 178610), 4 com. left tbt. (167274, 178442, 178444, 178605), 11 incom. left tbt. (167080, 167084, 167177, 167272, 167273, 167276, 178441, 178443, 178529, 178530, 178606), 7 prox. end left tbt. (167178, 167275, 167277, 167278, 167280, 178607, 178608), 8 com. right tmt. (167179, 167297, 167298, 178459, 178460, 178540, 178611, 178612), 3 incom. right tmt. (167296, 178461, 178462), prox. end right tmt. (167299), shaft frag. right tmt. (178465), dist. end right tmt. (178541), 6 com. left tmt. (167180, 167291, 167292, 178455, 178456, 178539), incom. left tmt. (167293), shaft frag. left tmt. (178458).

APPENDIX V

Measurements of *Gallinula mortierii* from Amphitheatre Cave. The measurement for the proximal width of the tibiotarsus PW = the distance between the medial edge of the *fac. art. medialis* and the lateral edge of the *fac. art. lateralis.*

	μ	s-1	OR	N
HUMERI				
Greatest Length [GL]	63.6	2.2	60.0 - 67.9	21
Proximal Width [Bp]	13.7	0.6	12.7 - 14.8	22
Distal Width [Bd]	9.9	0.5	9.0 - 10.9	21
ULNAE				
Greatest Length [GL]	46.7	1.6	43.6 - 48.9	13
CARPOMETACARPI				
Greatest Length [GL]	35.7	1.2	33.3 - 37.6	16
FEMORA				
Length [Lm]	79.4	2.6	74.6 - 83.0	25
Proximal Width [Bp]	17.3	0.7	16.1 - 18.7	24
Distal Width [Bd]	16.4	0.5	15.6 - 17.5	24
TIBIOTARSI				
Length [La]	130.0	4.2	121.9 - 137.2	29
Proximal Width [PW]	14.5	0.6	13.4 - 16.0	26
Distal Width [Bd]	12.4	0.5	11.5 - 13.5	31
TARSOMETATARSI				
Greatest Length [GL]	85.7	3.7	78.4 - 90.5	37
Proximal Width [Bp]	13.3	0.4	12.5 - 14.7	32
Distal Width [Bd]	13.4	0.4	12.6 - 14.5	36
CORACOIDS				
Length [Lm]	35.7	1.2	33.6 - 37.9	13

APPENDIX VI

Length measurements of fossil *Dasyornis* postcranial material from Amphitheatre Cave. The measurement for humerus length, L, equals the distance between the *caput humeri* and the *cond. ventralis* (see Table 3 for the Greatest Length measurements).

	μ	s-1	OR	N
HUMERI				
Length [L]				
D. brachypterus	20.6	0.8	19.8 - 21.5	4
D. broadbenti	25.5	0.8	24.3 - 27.0	22
ULNAE				
Greatest Length [GL]				
D. brachypterus	17.1	0.7	16.6 - 17.6	2
D. broadbenti	21.7	0.6	20.7 - 22.4	8
FEMORA				
Greatest Length [GL]				
D. brachypterus	25.6	0.5	25.1 - 26.6	8
D. broadbenti	30.7	1.0	28.9 - 32.3	26
TIBIOTARSI				
Length [La]				
D. brachypterus	37.4	1.2	36.0 - 38.9	4
D. broadbenti	48.2	1.9	44.4 - 52.4	26
TARSOMETATARSI				
Greatest Length [GL]				
D. brachypterus	26.6	1.0	26.0 - 28.1	4
D. broadbenti	35.1	1.1	33.6 - 37.6	18

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Two New Species of *Periclimenes* (Crustacea: Decapoda: Palaemonidae) from Lizard Island, Queensland, with Notes on Some Related Taxa

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Abstract. Two new species of *Periclimenes* caught in traps at Lizard Island, Queensland, *P. lacertae* and *P. priodactylus*, are described. *Periclimenes denticulatus* Nobili, *P. agag* Kemp and *Periclimenes laccadivensis* (Alcock & Anderson) are reported from Australia for the first time. Further information is presented on other Australian specimens of *Periclimenes, P. platycheles* Holthuis, *P. attenuatus* Bruce, *P. amboinensis* (De Man), and on *Parapontonia nudirostris* Bruce, with remarks on some non-Australian specimens of *Periclimenes, P. lanipes* Kemp, *P. pholeter* Holthuis and "*P. consobrinus*" Balss (*non* De Man). The extraordinary occurrence of *P. pholeter* in traps at 1825 m in the Red Sea, previously known only from anchialine habitats, represents the greatest depth from which a palaemonid shrimp has so far been recorded. Its first occurrence in the western Pacific Ocean is also recorded.

Bruce, A.J., 1992. Two new species of *Periclimenes* (Crustacea: Decapoda: Palaemonidae) from Lizard Island, Queensland, with notes on some related taxa. Records of the Australian Museum 44(1): 45–84.

Very few pontoniine shrimps have been reported from traps and the few records have been of deep-water species. It is therefore of interest that small traps set in shallow water at Lizard Island, Queensland, by Dr J.K. Lowry and S.J. Keable, have provided specimens of two undescribed species of *Periclimenes, P. lacertae* n.sp., and *P. priodactylus* n.sp., and one very poorly known species, *P. denticulatus* Nobili. Other *Periclimenes* species of interest were also caught in the traps, and are discussed in this report. Further pontoniine material also included in this report is derived from a study of the commensal associates of crinoids on the northern Great Barrier Reef carried out by Ms K. Fabricius. The first Australian specimen of *Periclimenes laccadivensis* (Alcock & Anderson) from 720 m, off Cape Freycinet, Tasmania, is also reported. Additional information is also provided upon the *Pola* Expedition material referred to *P. consobrinus* by Heinrich Balss (1915) and on specimens of *P. brocki* from Singapore Straits by Johnson (1961, 1979). Recent collections of *P. pholeter* from deep-water traps in the central Red Sea, from R.V. *Meteor* material, are also recorded and further specimens

are also reported from shallow anchialine water from Fiji, the first occurrence of this species in the Western Pacific Ocean.

Carapace length (CL) refers to the postorbital carapace length. Abbreviations for institutions are as follows: AM – Australian Museum, Sydney; NTM – Northern Territory Museum, Darwin; NHMV – Naturhistorisches Museum, Wien; NMV – Museum of Victoria, Melbourne; RMNH – Rijksmuseum van Natuurlijke Historie, Leiden.

The species examined in this paper are: *Periclimenes lacertae* n.sp., *Periclimenes priodactylus* n.sp., *Periclimenes denticulatus* Nobili, 1906, *Periclimenes platycheles* Holthuis, 1952, *Periclimenes agag* Kemp, 1922, *Periclimenes amboinensis* (De Man, 1888), *Periclimenes attenuatus* Bruce, 1971, *Periclimenes laccadivensis* (Alcock & Anderson, 1894), "*Periclimenes consobrinus*" Balss, 1915, *Periclimenes pholeter* Holthuis, 1973, *Periclimenes lanipes* Kemp, 1922, and *Parapontonia nudirostris* Bruce, 1968.

Periclimenes lacertae n.sp.

Figs 1-6

Material examined. 1 male, stn Qld-197, off Chinaman's Ridge, Mrs Watson's Bay, Lizard Island, 22-33 m, trap, 20-21 Jan. 1989, coll. J.K. Lowry, S.J. Keable.

Description. Medium-sized shrimp, slender subcylindrical body form.

Carapace glabrous, smooth, with rostrum long, slender, straight, horizontal, about 1.85 times carapace length, lateral carinae obsolete, dorsal margin with 10 acute teeth, first tooth slightly anterior to posterior orbital margin, first 10 evenly spaced, distal 2 smaller, closer, subterminal interspaces with 2-3 short setae proximally, lower margin with 6 acute teeth, first situated below fourth dorsal tooth, of slightly decreasing size and spacing distally, interspaces with double row of numerous setae, proximal to first ventral tooth with single median row of setae; epigastric tooth present, slightly posterior to level of hepatic tooth, supraorbital spines absent, orbit obsolete, inferior orbital angle distinct, feeble, antennal spine slender, acute, marginal, below level of inferior orbital angle, hepatic spine slender, acute, below level of antennal spine, at about 0.15 of carapace length, anterolateral angle of branchiostegite bluntly obtuse.

Abdomen glabrous, smooth, third segment not posterodorsally produced, fifth segment about 0.5 of length of sixth, sixth moderately compressed, about 1.5

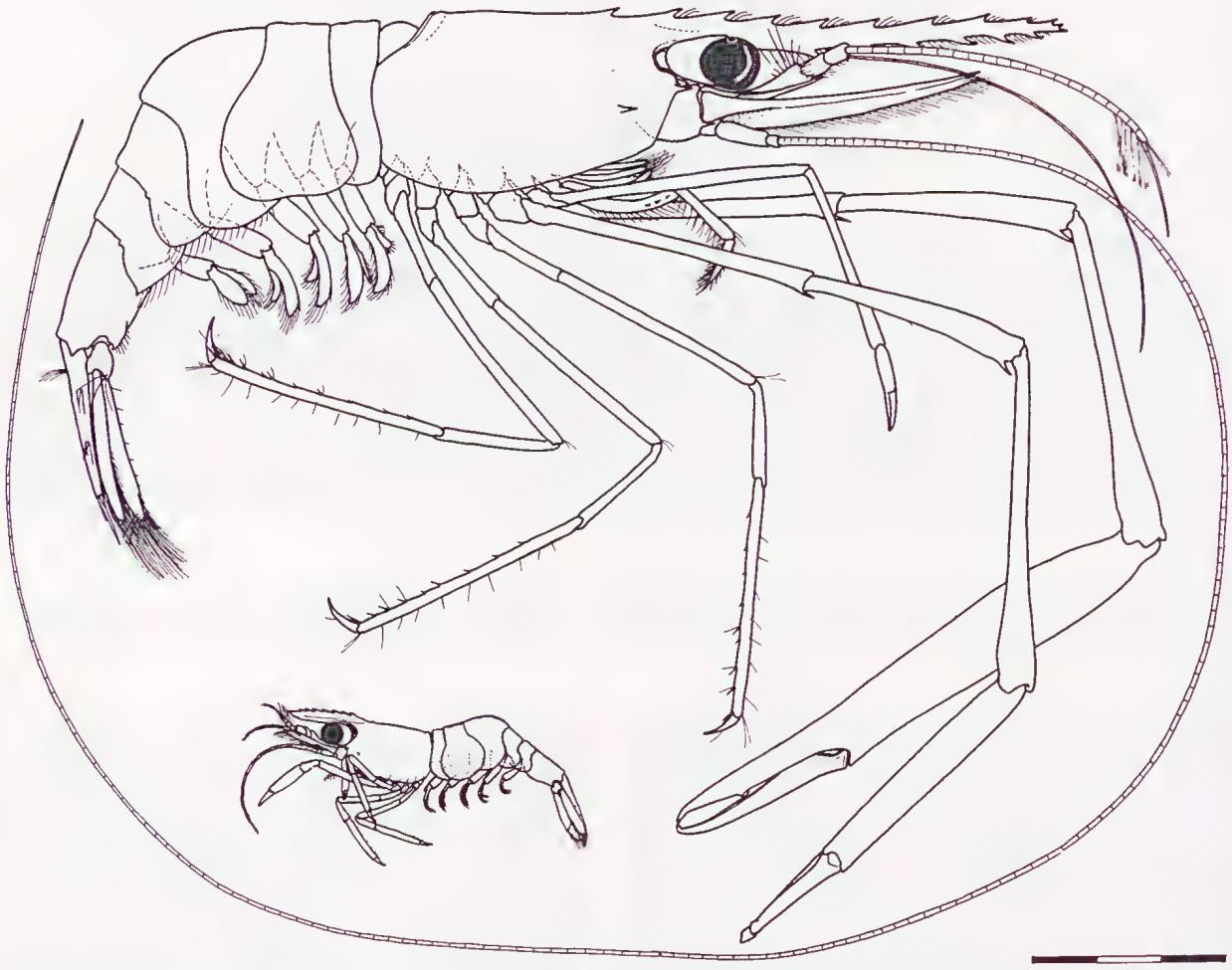

Fig.1. *Periclimenes lacertae* n.sp., holotype male, Lizard Island, Queensland, scale bar in millimetres. Inset, *P. priodactylus* n.sp., at same scale.

times longer than deep, subuniform, posterolateral angle produced, acute, posteroventral angle produced, with small acute posterior tooth, ventral margin setose, pleura of first 3 segments broadly rounded, fourth slightly posteriorly produced, rounded, fifth posteriorly produced, posteroventral angle acutely pointed, third to fifth pleura with ventral margins setose; telson about 1.4 of sixth segment length, about 3.0 times longer than

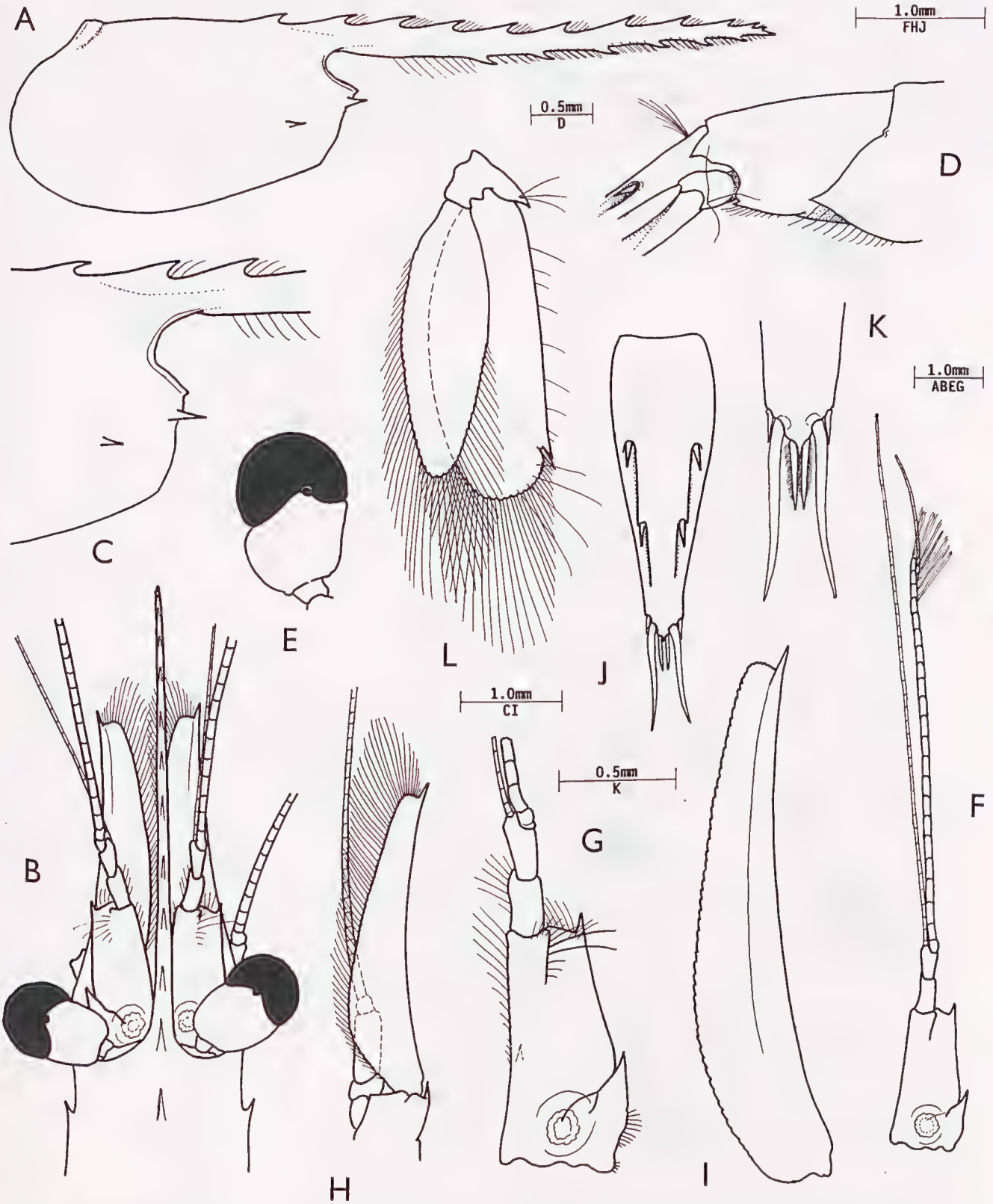

Fig.2. *Periclimenes lacertae* n.sp., holotype male. A, carapace and rostrum; B, anterior carapace, rostrum, eyes and antennal peduncles, dorsal; C, orbital region, lateral; D, posterior abdomen, lateral; E, eye; F, antennule; G, same, peduncle; H, antenna; I, scaphocerite; J, telson; K, same, posterior spines; L, uropod.

wide, maximum width at about 0.3 of length, lateral margins sinuous, posteriorly convergent, with 2 pairs of stout dorsal spines, at 0.33 and 0.6 of telson length, set proximally in deep longitudinal grooves, spines about 0.85 of telson length, posterior margin about 0.35 of telson width, acute, with acute median point, with 3 pairs of spines, lateral spines smaller than dorsal spines, about 0.2 of intermediate spine length, intermediate spines long, sinuous, 0.3 of telson length, 7.0 times longer than wide, submedian spines short, stout, straight, very acute distally, 0.43 of intermediate spine length, 7.0 times longer than proximal width, finely setulose medially and laterally.

Eye with large, globular, cornea well pigmented, with small dorsal accessory pigment spot; stalk moderately compressed, about as wide as long, length about 0.8 of corneal diameter.

Antennule with peduncle reaching to halfway between fourth and fifth dorsal rostral teeth; proximal segment about 2.2 times longer than wide, medial margin straight, setose, with acute ventral tooth at 0.45 of length, lateral margin feebly concave, convergent distally, distolateral angle not produced, setose ventrally, with acute distolateral tooth; stylocerite short, acute, reaching to 0.4 of segment length, lateral margin proximally with short plumose setae; statocyst well developed, with

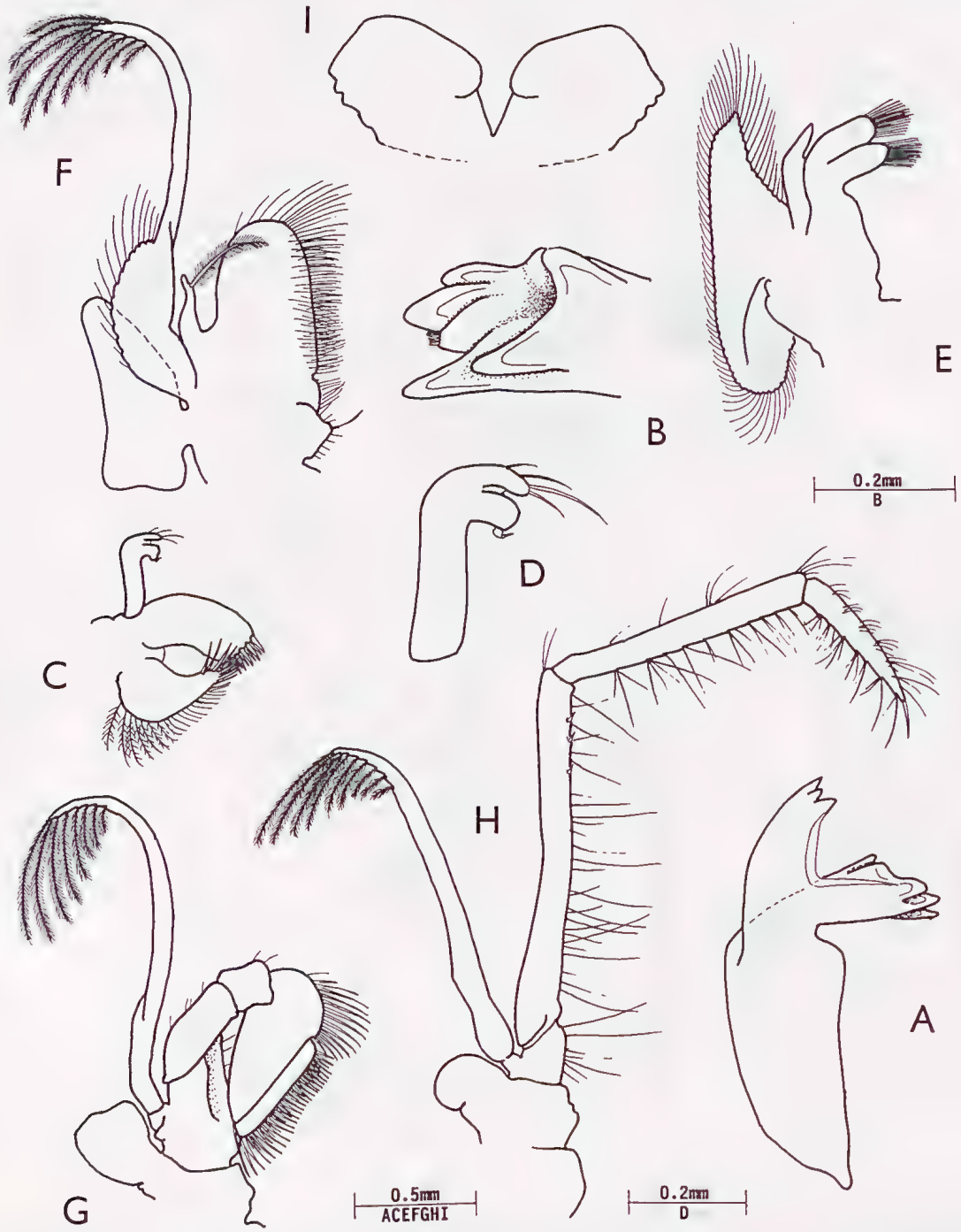

Fig.3. *Periclimenes lacertae* n.sp., holotype male. A, mandible; B, same, molar process; C, maxillula; D, same, palp; E, maxilla; F, first maxilliped; G, second maxilliped; H, third maxilliped; I, paragnaths.

discoid statolith; distal dorsal surface with longitudinal row of setae, with 2 very long, densely setulose; intermediate segment 1.8 times longer than wide, 0.25 of proximal segment length, with small medial setose lamella; distal segment about 1.2 times intermediate segment length, 2.0 times longer than distal width,

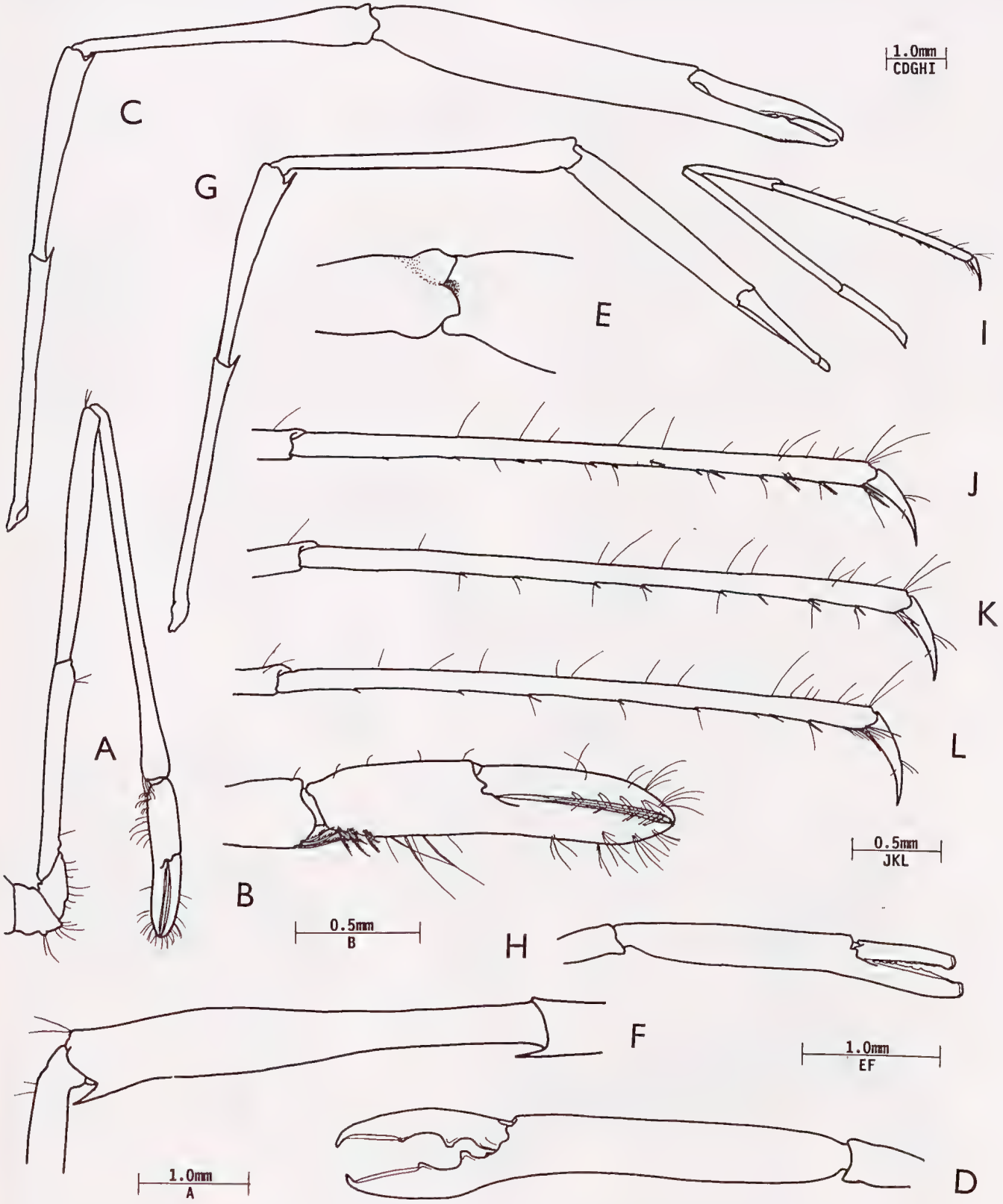

Fig.4. *Periclimenes lacertae* n.sp., holotype male. A, first pereiopod; B, same, chela; C, major second pereiopod; D, same, chela; E, same, carpopropodal joint, F, same, merus; G, minor second pereiopod; H, same, chela; I, third pereiopod; J, same, propod and dactyl; K, fourth pereiopod, propod and dactyl; L, fifth pereiopod, propod and dactyl.

slightly narrower proximally; upper flagellum biramous, with rami fused for proximal 20 segments, very long and slender, short ramus, including fused portion, 1.46 times of carapace length, with 2 free segments, with 9 groups of aesthetascs; longer ramus with 6 segments, very slender; lower flagellum about 1.5 times length of short upper ramus length, very slender.

Antenna with stout basicerite, with slender acute distoventral lateral tooth; carpocerite stout, 2.5 times longer than wide; ischiocerite, basicerite normal,

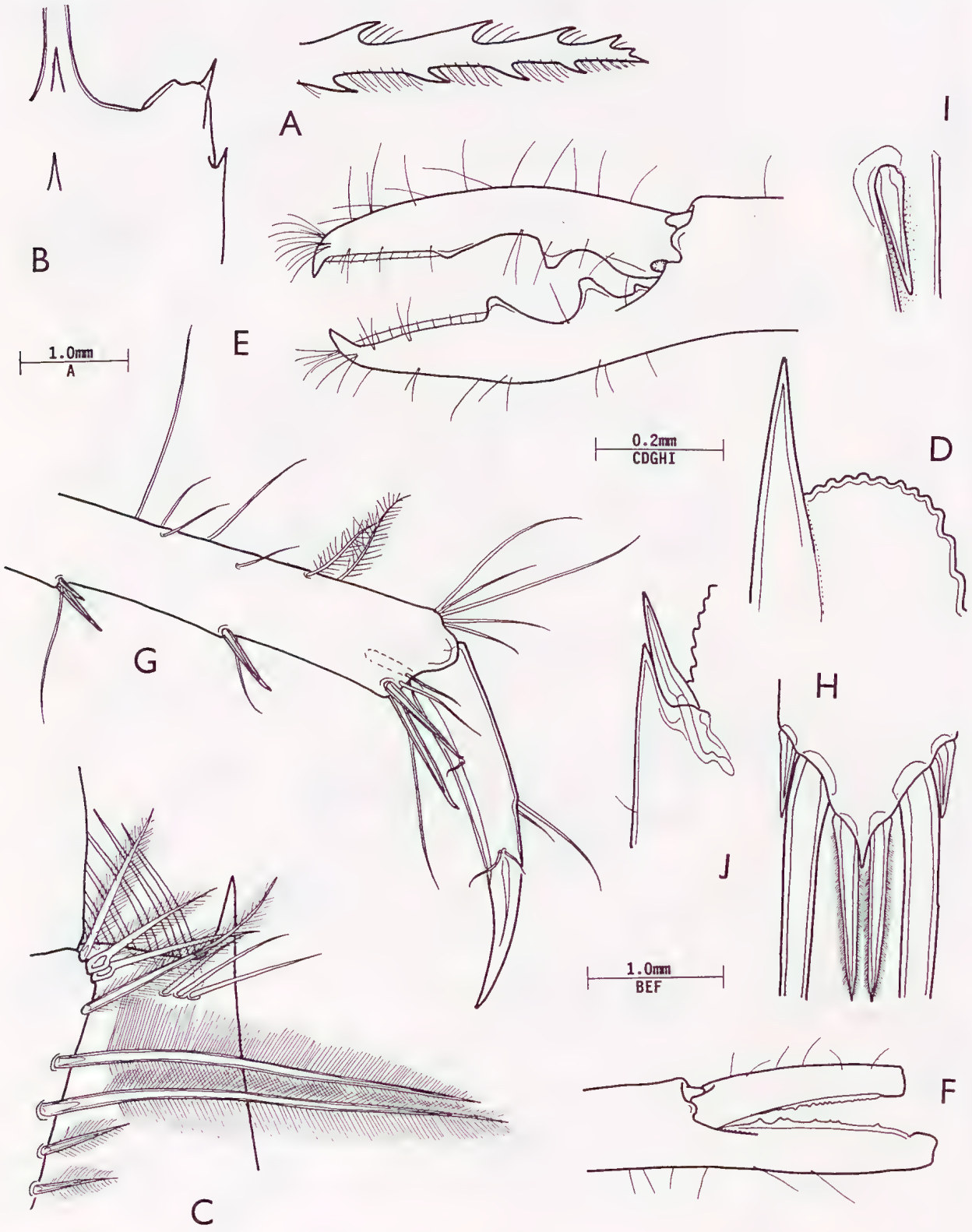

Fig.5. *Periclimenes lacertae* n.sp., holotype male. A, distal rostrum; B, right orbital region, dorsal; C, antennule, distolateral proximal segment; D, distal scaphocerite; E, major second pereiopod, fingers; F, minor second pereiopod, fingers; G, third pereiopod, distal propod and dactyl; H, telson, posterior spines; I, same, distal spine; J, exopod of uropod, distolateral angle.

flagellum elongate, slender, about 12 times carapace length; scaphocerite reaching to about level of seventh dorsal rostral tooth, about 5.8 times longer than maximal width, at about 0.3 of length, tapering strongly distally, lateral margin concave, with strong acute distal tooth, far exceeding anterior margin of lamella, distal margin of lamella bluntly subrectangular, about 0.38 of maximum width.

Ophthalmic somite without bec ocellaire; epistome unarmed; first to third thoracic sternites broad, unarmed, fourth with slender median process, fifth with transverse carina with deep median notch, sixth to eighth broad, unarmed.

Mandible (right) without palp; corpus stout, molar process expanded distally, obliquely truncate, with 5 stout blunt teeth, with smaller rounded posterior lobe with several short stout setae, incisor process short, stout, with 3 stout acute distal teeth, medial tooth largest, central tooth smallest, medial edge carinate, extending onto molar process; maxillula with slender palp, deeply bilobed distally, upper lobe slender with 4 setae laterally, lower lobe stouter, with small ventral process with single short terminal seta; upper lacinia curved, with about 10 short simple spines distally, with transverse row of short serrulate setae proximally; lower lacinia tapering, with numerous serrulate spiniform setae distally, ventral margin setose, plumose setae proximally; maxilla with simple, tapering palp, basal endite deeply bilobed, lobes subequal, with dense tuft of simple setae distally, coxal endite obsolete, scaphognathite normal, about 3.5 times longer than wide, posterior lobe broad, about 1.4 times longer than wide, anterior lobe tapering distally, 1.5 times longer than wide, medial margin concave; first maxilliped with short, slender, tapering palp with long densely plumose preterminal seta medially, basal endite large, broadly rounded, separated by small notch from coxal endite, large, broadly rounded, medial margin densely setose, coxal endite bilobed, distal lobe rounded, with numerous setae, proximal lobe angular with stout apical seta, several short setae, exopod with well-developed flagellum with numerous plumose setae distally, caridean lobe small, epipod large, distal portion tapering, blunt, posterior part truncate; second maxilliped with normal endopod, dactylar segment narrow, densely

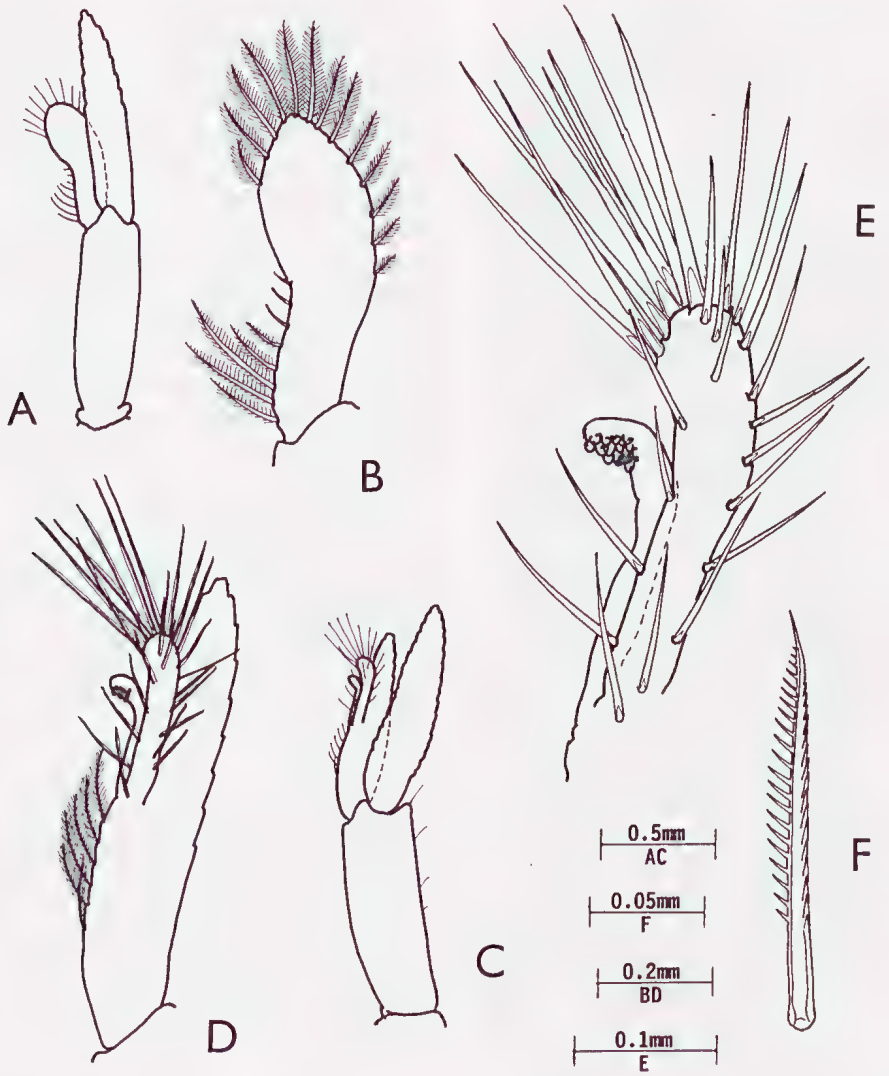

Fig.6. *Periclimenes lacertae* n.sp., holotype male. A, first pleopod; B, same, endopod; C, second pleopod; D, same, endopod; E, same, appendix masculina and appendix interna; F, third maxilliped, distal segment of endopod, ventral spine.

margined with short stout, serrulate spines, propodal segment broad, anteromedial margin rounded with about 12 long slender spines, carpus and ischiomerus normal, basis medially excavate, exopod with well-developed flagellum with numerous plumose setae distally, coxa feebly produced medially, non-setose, trapezoid epipod laterally, without podobranch; third maxilliped with endopod slender, exceeding carpocerite by about 0.5 of terminal segment, ischiomerus slender, about 11.0 times longer than distal width, moderately bowed, distal half subcylindrical, with 3 small lateral spines, proximal half slightly swollen, medial margin with sparse long simple setae, penultimate segment 0.75 of proximal segment length, subcylindrical, 9.0 times longer than distal width, with sparse spiniform setae ventrally, distal segment about 0.4 of proximal segment length, tapering distally, 5.0 times longer than proximal width, with stout simple apical spine, sparse groups of stout serrulate spines ventrally, basis not medially produced, sparsely setose, exopod with well developed flagellum with numerous plumose setae distally, coxa feebly produced medially, non-setose, with small rounded lateral plate, without arthrobranch.

First pereiopod long, slender, exceeding carpocerite by about distal tenth of merus; chela with palm subcylindrical, slightly compressed, 2.5 times longer than deep, uniform with 5 groups of short serrulate cleaning setae proximoventrally and several long simple setae, fingers slightly longer than palm with small acute hooked tips, distal 0.8 of cutting edges sharp, entire, simple, feebly laterally situated, with numerous groups of short setae; carpus 2.4 times chela length, proximal 0.8 subuniform, distal 0.2 slightly swollen, about 12.5 times longer than distal width, unarmed, with 4 long serrulate cleaning setae distoventrally; merus about 0.66 of carpus length, 10.0 times longer than maximum width, at about 0.75 of length, unarmed; ischium 0.46 of merus length, about 9.5 times longer than distal width, uniform, unarmed; basis short, unarmed, about 0.16 of carpus length, sparsely setose ventrally; coxa normal, without ventral process.

Second pereiopods very well developed, elongate, slender, unequal, chelae dissimilar; major chela 2.5 times carapace length, palm smooth, subcylindrical, about 5.7 times longer than maximum depth, very feebly swollen proximally, fingers equal to 0.5 of palm length, compressed, expanded centrally, with stout, hooked tips, dactyl about 4.6 times longer than depth at level of major tooth, cutting edge distally entire, sharp, with small tooth at 0.6 of length, separated from major tooth at 0.3 of length by large U-shaped notch, with smaller similar notch proximally, with dactylar fossa present proximally, fixed finger similar, with distal tooth larger, opposing into larger dactylar notch and major tooth into proximal dactylar notch, all teeth distally blunt, major teeth truncate distally; carpus about 0.9 of palm length, proximal two thirds slender, distal third swollen, about 7.5 times longer than distal width, distal margin feebly bilobed dorsally, unarmed; merus 0.64 of palm length, 6.5 times longer than distal width, distally expanded, distal half slightly swollen, 1.8 times wider than proximal width, with large slender acute distoventral tooth; ischium slender, 0.83 of palm length, 12.5 times longer than distal width, slightly tapered proximally, with large slender acute distoventral tooth; basis and coxa normal; minor chela with palm about 1.18 of carapace length, 0.45 of major chela length, palm about 5.5 times longer than deep, smooth, subcylindrical, uniform, fingers damaged, tips lacking, more than 0.5 of palm length, dactyl with sharp cutting edge with numerous irregular very small denticles, fixed finger with fewer, more acute small teeth; carpus 1.36 of palm length, subequal to major carpus length, similar, more slender, about 10.0 times longer than distal width, slightly swollen distally; merus and ischium similar to major chela, subequal, slightly more slender.

Ambulatory pereiopods slender; third pereiopod exceeding carpocerite by distal 0.2 of merus, rostrum by dactyl and distal fourth of propod; dactyl, compressed, curved, without distinctly demarcated unguis, 5.6 times longer than proximal depth, simple, with 1 long, 1 short simple setae at 0.5 of dorsal margin length, pair of sensory setae distomedially and distolaterally, about 0.14 of propod length; propod about 1.06 times carapace length, slender, uniform, unsegmented, about 23.0 times longer than distal width, with pair of strong distoventral spines, 11 spines spaced along ventral margin, distal spines well developed, smaller than distoventral spines, proximal spines small; carpus about 0.39 of propod length, with distinct distodorsal lobe, about 6.5 times longer than distal width, unarmed; merus about 0.92 of propod length, about 17.5 times longer than wide, uniform, unarmed; ischium about 0.33 of propod length, about 6.4 times longer than distal width; basis and coxa without special features; fourth and fifth pereiopods similar to third, propod of fourth slightly longer, 1.06 times third propod length, slightly more feebly spinulate ventrally, fifth propod with medial distoventral spine only, with 4 pairs of distolateral cleaning setae.

First pleopod with basipodite 3.5 times longer than broad; exopod subequal to basipodite length, 5.5 times longer than proximal width; endopod about 0.58 of exopod length, 4.0 times longer than central width, distal half expanded, proximal half of medial margin with few serrulate spiniform setae proximally, 3 short simple spines distally, distal fourth of medial margin and distal half of lateral border with 13 short plumose setae. Second pleopod with basipodite 3.0 times longer than broad, subequal to first basipodite length, exopod subequal to basipodite length, 4.0 times longer than central width; endopod about 0.88 of exopod length, about 4.2 times longer than central width, with appendices at 0.5 of medial margin length; appendix masculina about 0.3 of endopod length, subcylindrical, about 5.5 times longer than central width, slightly swollen and medially curved, with about 10 short slender spines along lateral margin, 4 along medial margin, 3 distoventrally, 8 stout slender simple spines distally, longest about 0.8 of corpus length, appendix interna about 0.75 of appendix masculina length, with few distal cincinnuli.

Uropod with protopodite posterolaterally acute; exopod about 2.6 times longer than wide, extending well beyond tip of telson, lateral margin straight, unarmed, sparsely setose, with small acute distal tooth with larger acute mobile spine medially, diaeresis obsolete; endopod 0.91 of exopod length, about 3.15 times longer than broad.

Measurements (mm). Total length (approx.) 21.0; carapace and rostrum 10.2; carapace 3.6; major second pereiopod chela 8.8; minor second pereiopod chela 6.0+.

Type. The single male specimen is designated as holotype and deposited in the AM collection, registration number P39299.

Colouration. No data.

Etymology. From *lacerta* (latin), a lizard, in reference to locality of capture, Lizard Island.

Systematic position. *Periclimenes lacertae* is most closely related to *P. tenuipes* Borradaile, 1898, first reported from New Britain and subsequently widely recorded throughout most of the Indo-west Pacific region, and which itself occupies a rather isolated position in relation to other species of the genus. Both species are members of the "*P. grandis* species group" *sensu latu*, with a well-developed, finger-like median process on the fourth thoracic sternite and have well-developed meral spines on the second pereiopods, lack supraorbital spines and have slender ambulatory pereiopods with slender, not strongly curved dactyls. *Periclimenes lacertae* is immediately distinguished from all related species by the presence of slender distoventral ischial tooth on the second pereiopods. Other features in which it differs from *P. tenuipes* are that the rostrum is straight and horizontal, not sinuous and up-curved, with a similar dentition of 10/6, compared with 8-11/6-9 in *P. tenuipes*. In *P. tenuipes*, the ambulatory propods are reported to be segmented and devoid of spines (Kemp, 1922), but show no signs of segmentation and are distinctly spinose in *P. lacertae*. The pleuron of the fourth abdominal somite appears more rounded, less angular, in *P. lacertae*, and that of the fifth, more acutely pointed than in Kemp's figure (pl.8 fig.11).

Remarks. *Periclimenes ischiospinosus* Bruce, known only from two specimens from New Caledonia (Bruce, 1991), is the only other Indo-west Pacific species of *Periclimenes* to have an ischial spine on the second pereiopods. In its general morphology it shows a close similarity to *P. lacertae* but does not belong to the "*P. grandis* group", and lacks a median process on the fourth thoracic sternite. Both specimens of *P. ischiospinosus* have damaged rostra and detailed comparison is therefore not possible. *P. ischiospinosus* also occurs in deeper water, from 50 m.

A key to the species of the "*P. grandis* group" has been provided by Bruce (1987). *Periclimenes lacertae* can be readily incorporated by means of the following couplets:

12. Rostrum greatly exceeding scaphocerite 12a

—— Rostrum subequal to scaphocerite 13

12a. Second pereiopods with ischium distoventrally unarmed. rostrum sinuous, upcurved, ambulatory propods segmented, non-spinulate; R. 1+8-11/6-9 .....*P. tenuipes* Borradaile

—— Second pereiopods with strong distoventral ischial tooth; rostrum straight, horizontal; ambulatory propods not segmented, spinulate; R. 1+10/6 .....*P. lacertae* n.sp.

Periclimenes priodactylus n.sp.

Figs 1, 7-11

Material examined. 1 male, stn Qld-320, Lizard Island, Queensland, 14°40'S 145°28'E, northern entrance to Blue Lagoon, Lizard Island, 3.5 m, trap, 6-7 June 1989, coll. S.J. Keable, D.J. Townsend.

Description. Very small-sized shrimp, subcylindrical body form.

Carapace smooth, glabrous, with well-developed, compressed rostrum, subequal to carapace length, slightly exceeding antennular peduncles, horizontal, distally acute tip slightly upturned, well-developed feebly convex dorsal carina with 7 acute teeth, all anterior to posterior orbital margin, regularly spaced, size decreasing slightly distally, lateral carinae well developed, broadening posteriorly, ventral carina feebly developed, ventral margin straight, non-setose, with single very small acute tooth distally, below seventh dorsal tooth; epigastric and supraorbital spines absent, with small postorbital tubercle, orbital notch broad, orbit obsolete, inferior orbital angle feebly produced, broadly rounded, antennal spine small, submarginal, hepatic spine small, slender, ? mobile, slightly below level of antennal spine, anterolateral branchiostegite not produced, broadly rounded.

Abdomen smooth, glabrous, third segment feebly posterodorsally produced, sixth segment about 2.5 times longer than fifth, compressed, 1.5 times longer than deep, about 0.5 of carapace length, posteroventral angle slightly produced, subacute, posterolateral angle blunt; pleura of first 3 segments broadly rounded, fifth and sixth rounded, slightly posteriorly produced. Telson about 0.7 of carapace length, 3.0 times longer than anterior width, lateral margins sublinear, convergent, with 2 pairs of small marginal dorsal spines, about 0.045 of telson length, at 0.6 and 0.8 of telson length, posterior margin about 0.4 of anterior width, feebly angular, with median process, with 3 pairs of spines, lateral spines small, subequal to dorsal spines, intermediate spines

robust, about 0.16 of telson length, 4.5 times longer than wide, submedian spines well developed, very slender distally, 0.78 of intermediate spine length, distally densely setulose.

Antennule with peduncle slightly exceeded by rostrum, far exceeded by scaphocerite, proximal segment about 2.5 times longer than central width, medial margin with ventromedial tooth, stylocerite short, broad, acute, reaching about 0.4 of segment length, slightly laterally projecting, statocyst normally developed, with granular statolith; intermediate and distal segments short, subequal, together subequal to 0.45 of proximal segment length; upper flagellum small, short, biramous, proximal 2 segments fused, shorter free ramus 2 segmented, longer ramus 4 segmented, with 5 groups of aesthetascs; lower flagellum short, 6 segmented, subequal to peduncle length.

Antenna with basicerite unarmed; carpocerite short, stout, about 1.6 times longer than distal width, 0.25 of scaphocerite length, flagellum stout, robust, about 2.0 times carapace length, about 10 segments, obscurely segmented proximally; scaphocerite about 0.7 of carapace length, distinctly exceeding rostrum and antennular peduncles, about 3.3 times longer than central width, broad, distal lamella bluntly angular, lateral margin feebly concave, with slender distal tooth, far exceeded by lamella.

Eye large, with transverse hemispherical cornea, diameter about 0.33 of carapace length, with small dorsal accessary pigment spot; stalk about 1.2 times wider than corneal diameter, 1.1 times wider than length.

Ophthalmic segment without bec ocellaire, with conspicuous black pigment spot; epistome unarmed, fourth thoracic sternite without slender median process, posterior segments unarmed (?).

Mandible (right) with corpus moderately robust, without palp, molar process stout, with conspicuous blunt teeth distally, left molar process with row of stout distal spines, incisor process well developed, tapering distally, with distal margin transverse with 3 acute teeth, central tooth smaller than medial and lateral teeth; maxillula with short, stout, feebly bilobed palp, upper lobe small, lower lobe with short simple seta, upper lacinia normal, with 7 short, simple distal spines in 2 rows, with sparse short setulose setae, lower lacinia short, stout, tapering, blunt, with few serrulate distal setae; maxilla with slender simple tapering palp with short plumose setae proximolaterally, basal endite well developed, bilobed, lobes slender, with 4 simple setae distally, coxal endite obsolete, medial margin short, convex, scaphognathite well developed, about 3.0 times longer than wide, posterior lobe long, narrow, 3.0 times longer than anterior width, 0.33 of scaphocerite length, anterior lobe broad, about 1.3 times longer than wide, whole margin fringed with short, very stout, plumose setae; first maxilliped with slender simple, non-setose tapering palp, basal endite large, broad, distally rounded, medial margin straight, sparsely setose, with longer, feebly denticulate setae distally, shorter, sparsely denticulate setae proximally, coxal endite reduced, small, rounded, with 3 short feebly denticulate setae, 1 long, more strongly denticulate seta, exopod with well-developed flagellum, with 4 plumose setae distally, caridean lobe narrow, epipod lost in dissection (?); second maxilliped with normal endopod, dactylar segment about 2.8 times longer than broad, with few stout spines medially, strongly denticulate distally, propodal segment broad, with few short denticulate setae distomedially, sparse long feebly denticulate spiniform setae ventrally, carpus and merus normal, ischiomerus feebly excavate distomedially, exopod with well-developed flagellum, with 4 plumose setae distally, coxa feebly produced medially, with single short, simple seta, with small epipod laterally, without podobranch; third maxilliped with endopod slender, simple, reaching to about proximal end of carpocerite, ischiomerus and basis fused, junction

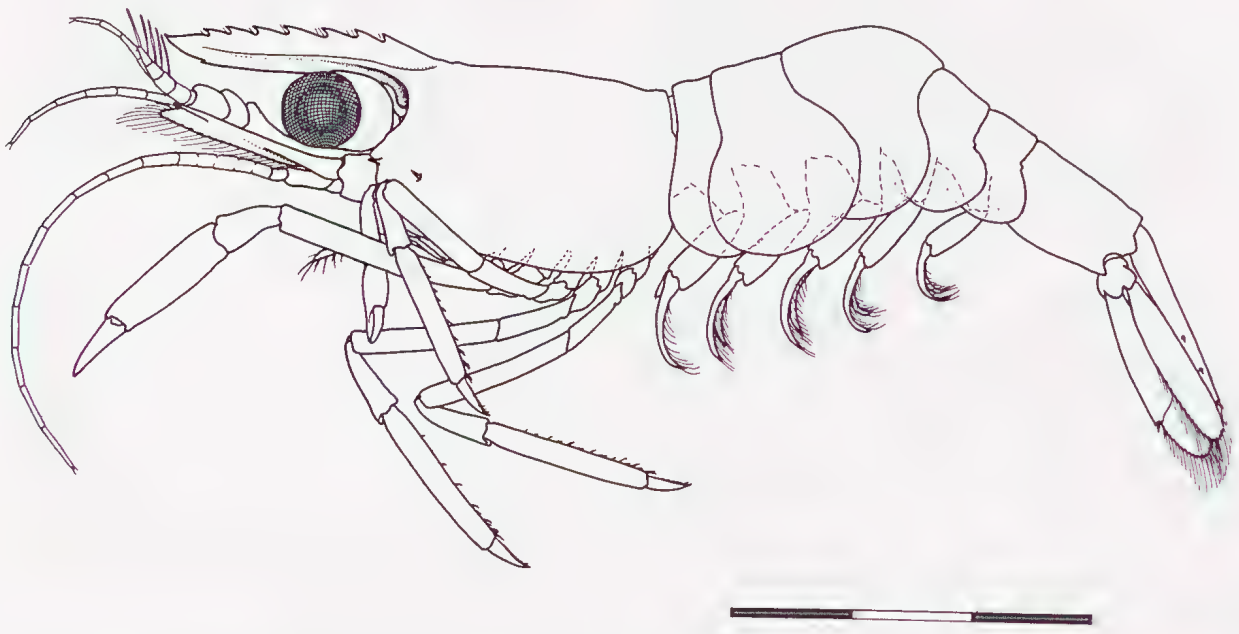

Fig.7. *Periclimenes priodactylus* n.sp., holotype male, Lizard Island, Queensland, scale bar in millimetres.

indicated by small median notch, combined segment bowed, about 4.8 times longer than distal width, slightly broadened distally, with basal region expanded, medially broadly convex, medial margin with sparse short simple setae, penultimate segment about 0.4 of proximal segment length, 2.8 times longer than wide, subuniform, with sparse long, feebly denticulate spiniform setae distally, with few similar setae ventrally, exopod with well-developed flagellum with 4 plumose setae distally, coxa with small angular medial process, with oval lateral plate, with vestigial arthrobranchial tubercle.

First pereiopod moderately short, stout, robust, exceeding carpocerite by length of chela; chela with palm subcylindrical, feebly compressed, slightly expanded distally, 1.5 times longer than distal width, with 2 serrulate cleaning setae proximally; fingers with strongly subspatulate cutting edges, lateral, entire, tips stout, moderately hooked, dactyl about 1.1 times palm length, 3.0 times longer than proximal depth, fixed fingers similar, carpus stout, about 0.58 chela length, 2.0 times longer than proximal width, slightly narrowed proximally, ventrally unarmed; merus about 0.8 of chela length, 1.5 times palm length, 5.0 times longer than wide, uniform, unarmed; ischium about 0.45 of chela

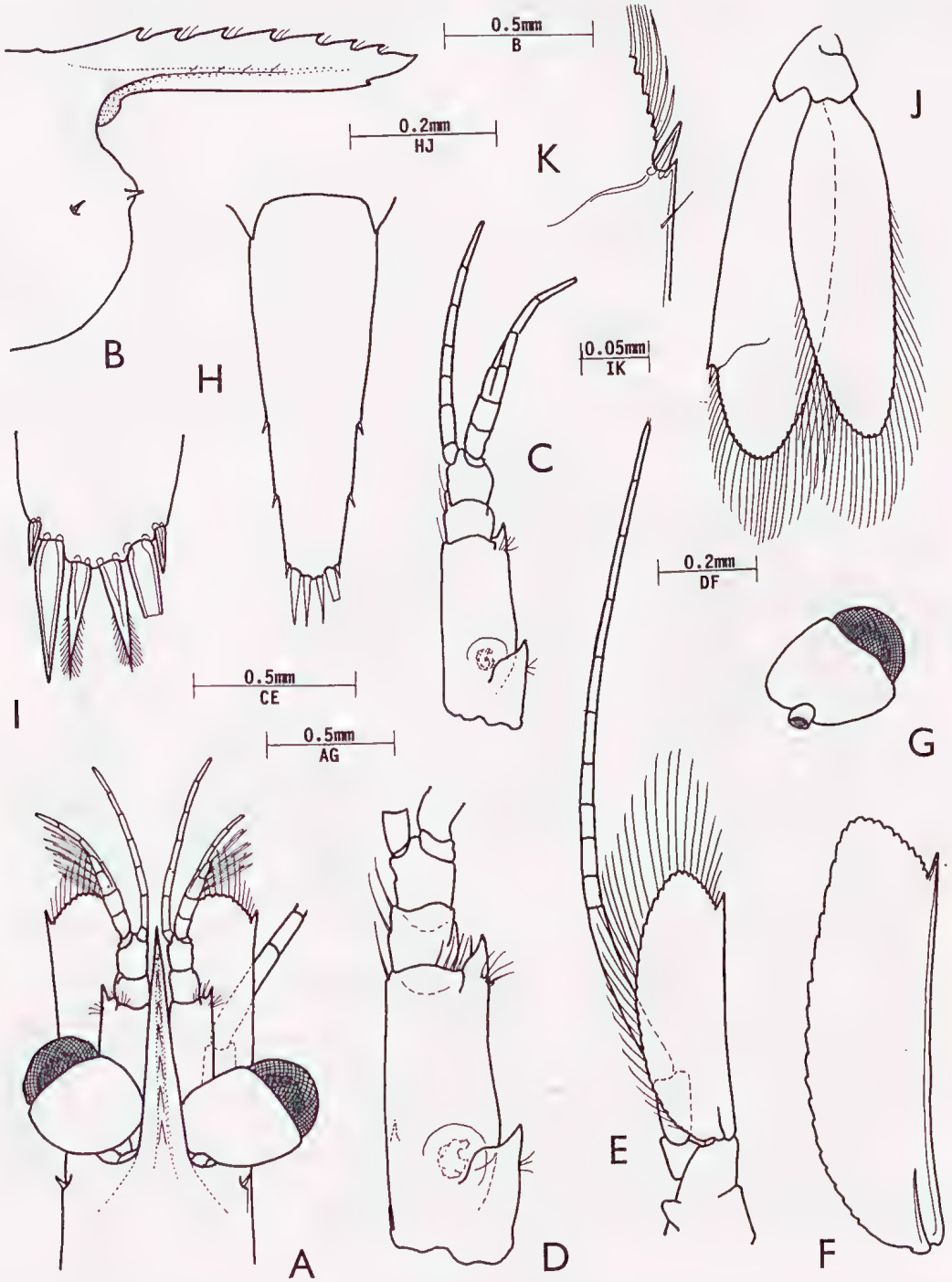

Fig.8. *Periclimenes priodactylus* n.sp., holotype male. A, anterior carapace, rostrum, eyes and antennae; B, anterior carapace and rostrum, lateral; C, antennule; D, same, peduncle; E, antenna, ventral; F, scaphocerite; G, eye; H, telson; I, same, posterior spines; J, uropod.

length, 2.2 times longer than distal width, obliquely articulated with basis, unarmed; basis about 0.7 of ischial length, unarmed; coxa with small setose ventral process.

Second pereiopods well developed, subequal, similar; chelae about 0.72 of carapace length, palm subcylindrical, smooth, about 2.75 times longer than distal depth, slightly compressed and broadened distally, dactyl about 0.7 of palm length, 3.3 times longer than proximal depth, tapering to stout feebly hooked, blunt tip, cutting edge lateral, distal half sharp, unarmed; carpus short, stout, about 0.45 of palm length, 1.4 times longer than distal width, slightly excavate distally, tapered proximally, unarmed; merus about 0.8 of palm length, 3.5 times longer than central depth, uniform, distoventral angle unarmed, bluntly rectangular; ischium subequal to meral length, about 3.4 times longer than distal width, tapered proximally, obliquely articulated with basis, unarmed; basis about 0.3 of palm length; coxa about 0.25 of palm length, both without special features.

Ambulatory pereiopods moderately robust; third pereiopod exceeding carpocerite by dactyl and most of propod, dactyl compressed, with unguis distinctly demarcated, slender, about 0.3 of corpus length, 5.5 times longer than proximal depth, tapering distally, dorsal margin convex, ventral margin straight, with well-developed distal accessory tooth, major part with series of very acute, compressed serrations, distally inclined, of increasing size distally, distolaterally with several

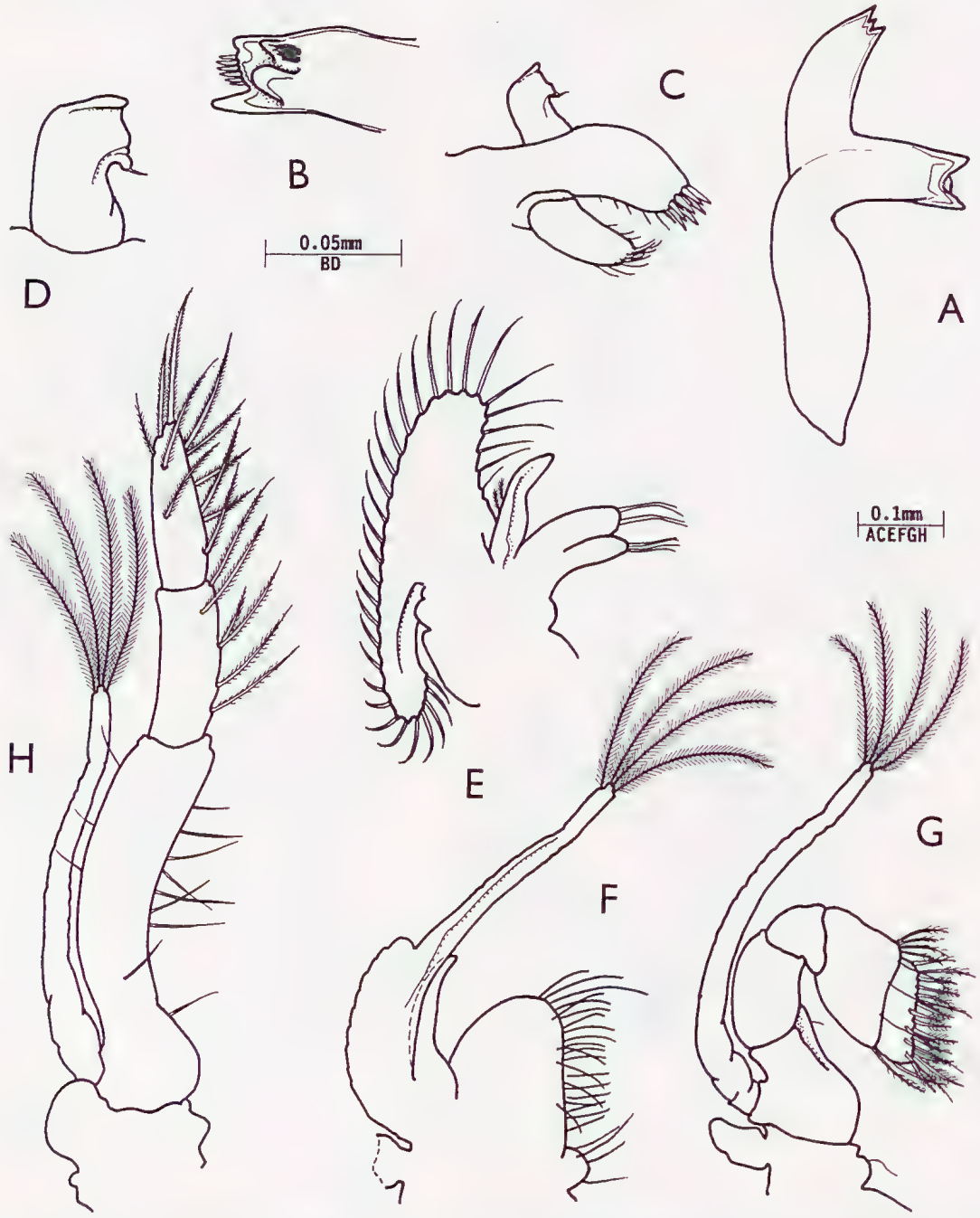

Fig.9. *Periclimenes priodactylus* n.sp., holotype male. A, mandible; B, same, molar process; C, maxillula; D, same, palp; E, maxilla; F, first maxilliped; G, second maxilliped; H, third maxilliped.

long simple setae; propod about 0.6 of carapace length, 3.5 times dactyl length, 6.0 times longer than central depth, distal half slightly tapered, with 3 distoventral spines, with single distolateral spine, 2 pairs of spines with offset medial and lateral ventral rows of 3 and 4 spines more proximally, spines sinuous, distoventrally denticulate, suberect posteriorly, distally inclined distally; carpus about 0.43 of propod length, 2.4 times longer than distal width, with strong distodorsal lobe, unarmed; merus about 0.85 of propod length, 5.0 times longer than deep, uniform, unarmed, distoventral angle bluntly rectangular; ischium about 0.5 of propod length, 3.0 times longer than distal width, unarmed; basis without special features; coxa with small setose ventral process. Fourth pereiopod similar to third, propod about 1.1 times third propod length, 6.0 times longer than deep, with distoventral pair of spines, medial and lateral ventral rows with 7 and 3 spines respectively. Fifth pereiopod similar to fourth.

First pleopod with basipodite 2.2 times longer than wide, exopod 1.2 times basipodite length, 4.4 times longer than wide, endopod about 0.36 of exopod length, 2.3 times longer than proximal width, medial margin straight, with single small spinule proximally, lateral margin convex, distally convergent to rounded tip, non-setose. Second pleopod with basipodite about 1.1 times first basipodite length, 2.3 times longer than wide, exopod 1.1 times basipodite length, 3.5 times longer than broad, endopod about 0.9 of exopod length, 3.8 times longer than wide, appendix masculina at 0.35 of endopod

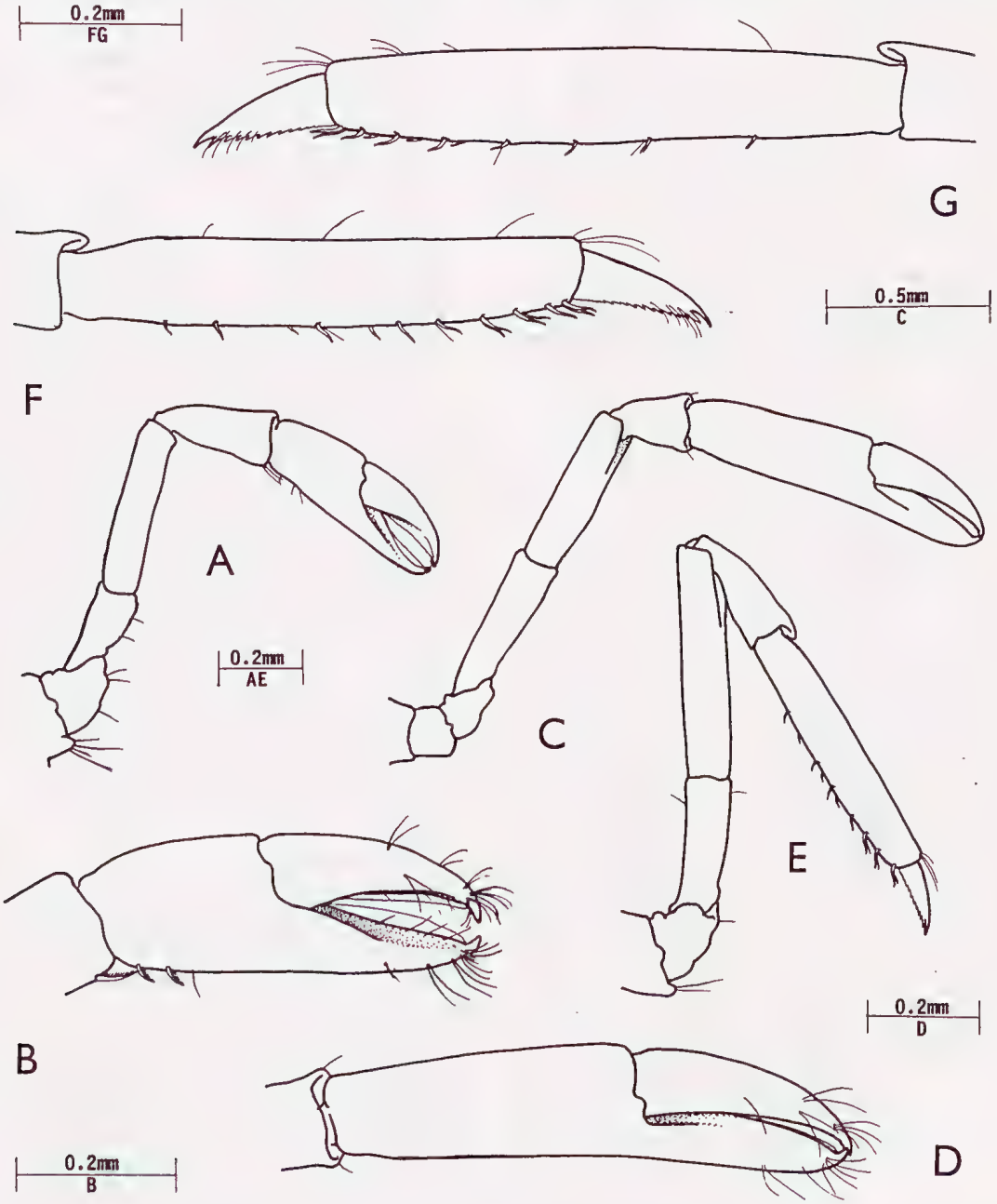

Fig.10. *Periclimenes priodactylus* n.sp., holotype male. A, first pereiopod; B, same, chela; C, second pereiopod; D, same, chela; E, third pereiopod; F, same, propod and dactyl; G, fifth pereiopod, propod and dactyl.

length, 0.45 of endopod length, distally swollen, cincinnuli not discernible, appendix masculina at 0.45 of endopod length, short, 0.22 of endopod length, subcylindrical, centrally swollen, 3.0 times longer than wide, with single long, simple terminal spiniform seta, 1.4 times corpus length, and shorter subterminal distolateral spiniform seta.

Uropod with protopodite distolaterally unarmed; exopod distinctly exceeding telson, 3.2 times longer than broad, lateral margin convex proximally, distally straight, with small acute distal tooth, with larger mobile spine medially, diaeresis feebly indicated; endopod about 0.9 of exopod length, 3.2 times longer than wide.

Measurements (mm). Total length (approx.) 4.75; carapace and rostrum 2.0; carapace 1.1; second pereiopod chela 0.8.

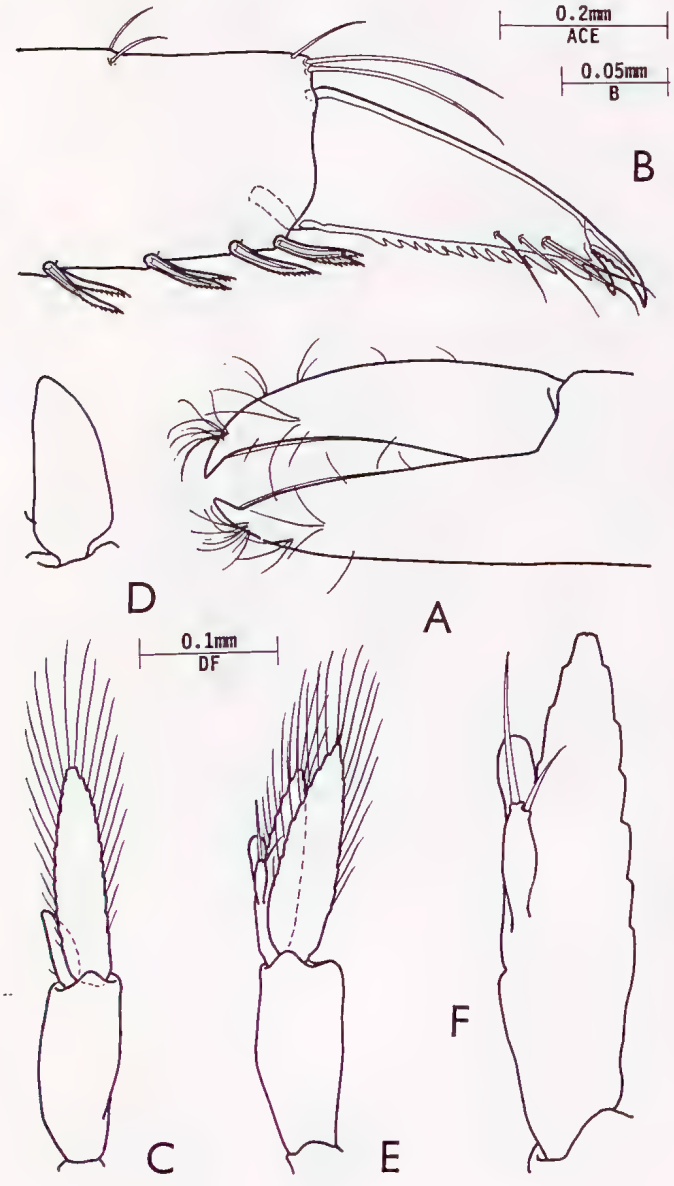

Fig.11. *Periclimenes priodactylus* n.sp., holotype male. A, second pereiopod, fingers; B, third pereiopod, dactyl and distal propod; C, first pleopod; D, same, endopod; E, second pleopod; F, same, endopod.

Type. The single male specimen is the holotype and is deposited in the AM collection, registration number P39435.

Host, colouration. No data.

Etymology. From *prion* (Greek) a saw; *daktylos* (Greek) finger, with reference to the morphology of the ambulatory dactyl.

Systematic position. *Periclimenes priodactylus* does not appear to be closely related to any of the so far described species of *Periclimenes*. The subspatulate fingers of the first pereiopod suggest an affinity to *P. imperator* Bruce, *P. rex* Kemp, *P. soror* Nobili or *P. pectiniferus* Holthuis but these all have the cutting edges of the first pereiopod fingers finely pectinate, and the dactyls of the ambulatory pereiopods are biunguiculate or simple, without ventral serrations. The only Indo-west Pacific species of *Periclimenes* with ventral serrations on the ventral border of the ambulatory dactyl corpus is *P. signatus* Kemp, 1925, of unknown associations, and known only from the male holotype specimen from the Andaman Islands. *Periclimenes signatus* lacks a subspatulate chela on the first pereiopods, has a rostral dentition of 10/1, with the first tooth posterior to the orbital margin, and a well-developed ventral tooth at half the ventral margin length, scaphocerite with distolateral tooth far exceeding lamella, antennal spine postmarginal, hepatic spine on same level as antennal, and fingers of second pereiopod strongly dentate. The ambulatory propods and dactyls show distinct similarities to *P. priodactylus*, with the dactyl biunguiculate, the ventral margin of the corpus microscopically serrate, the ventral margin of the propod densely spinulose, with about 24 spines in a single row illustrated in this position by Kemp (1925: fig.17d), and apparently all non-denticulate. The dactyl is only about 0.16 of the propod length and appears feebly serrated along the dorsal margin of the corpus or may have had a series of setae in this position. *Periclimenes signatus* is also a very small species, the specimen having a length of 11 mm, however, still distinctly larger than *P. priodactylus*.

Remarks. The specimen of *P. priodactylus* was caught by means of a small baited trap set overnight on the sandy lagoon floor, with numerous conical sand mounds. The traps have a funnel entrance of only about 1 cm and are baited with meat fragments. No echinoderms were captured.

Some recently described deep-water pontoniine shrimps from the North Atlantic Ocean, *Periclimenes milleri* and *P. ingressicolombi* (Bruce 1987a; Berggren & Svane, 1989) have ambulatory pereiopods resembling *P. priodactylus*, with numerous acute serrations along the ventral margin of the dactyl and the ventral propods with numerous denticulate spines. These species, observed and captured from submersibles, are known to associate with echinoid hosts, suggesting that *P. priodactylus* (and *P. signatus*) may be involved in similar

associations. *Allopontonia iaini* Bruce also has a series of fine serrations along the ventral margin of the ambulatory dactyls and is known to be an echinoid associate, its hosts being the temnopleurid urchins *Salmaciella dussumieri* and *Salmacis sphaeroides* and also diadematid urchins of the genus *Asthenosoma*.

Periclimenes priodactylus is noteworthy for its minute size, about the same as many first post-larval stage pontoniine shrimps, and its juvenile appearance is enhanced by the relatively large size of the eye. The presence of the appendix masculina shows that the specimen is not a juvenile and must represent a species that matures at a very small size. Other very small pontoniine shrimps have been reported: *Tectopontonia maziwiae*, ovigerous female, total length 8.0 mm (Bruce, 1973); *Typton nanus*, female 3.75 mm (Bruce, 1988)

Periclimenes denticulatus Nobili, 1906

Figs 12-14

Restricted synonymy

Periclimenes Petitthouarsi var. *denticulata* Nobili, 1906: 257-258.–Nobili, 1907: 358-359.
Periclimenes (Falciger) denticulatus.–Borradaile, 1917: 368, 372.
Periclimenes (Ancylocaris) denticulatus.–Kemp, 1922: 170, 197.
Periclimenes (Harpilius) denticulatus.–Holthuis, 1952: 11.
Palaemonella denticulata.–Holthuis, 1953: 55.
Periclimenes identiculatus.–Bruce, 1979: 230-231 (erroneous spelling for ? *denticulatus*).
Periclimenes denticulatus.–Devaney & Bruce, 1987: 223, 230.

Material examined. 1 male, stn Qld-135, off Coconut Beach, Lizard Island, 32 m, trap, on sand with *Halimeda*, 11-12 Jan. 1989, coll. J.K. Lowry and S.J. Keable, AM P39287 (*partim*).

Remarks. The single example lacks both second pereiopods and can not therefore be identified with absolute certainty. *Periclimenes denticulatus* is a little known species that has not yet been adequately described or illustrated, but the holotype specimen, unfortunately now in poor condition, is held in the collection of the Muséum National d'Histoire Naturelle, Paris (Na. 1944, CL. 3.0 mm) and, through the kindness of Prof. Jacques Forest, has been re-examined.

The Lizard Island specimen has the rostrum about 1.3 times its carapace length, moderately up-curved, with six acute dorsal teeth and three similar ventral teeth. The carapace has an epigastric tooth, a large marginal antennal spine and a smaller hepatic spine at a slightly lower level. The cornea of the eye is large and globular. The mandible bears a very small single-segmented palp, flattened, subcircular with two short simple lateral setae. The molar process is robust with two stout acute teeth distodorsally, with a broad posterior lobe, large, fringed with flattened setae. The incisor process is well developed, transversely truncate distally with three acute teeth, the central tooth smaller than the outer teeth, and a small preterminal medial tooth. The maxillula has a bilobed palp, the upper lobe with three short simple setae and the lower lobe with a small setose ventral tubercle. The upper lacinia is moderately broad, tapering, with about ten short simple spines distally and numerous short setae ventrally. The lower lacinia is short and broad, with several long spiniform setae distally and numerous setae ventrally. The maxilla has a simple palp, basal endite bilobed, coxal endite obsolete, scaphognathite short, posterior lobe narrow. The first maxilliped has a setiferous palp, basal endite broad, densely setose, coxal endite distinct, exopod with small caridean lobe, flagellum with numerous plumose setae distally and the epipod large and simple. The second maxilliped has a normal endopod, the flagellum of the exopod with numerous plumose setae distally: the epipod was probably lost in dissection. The third maxillipeds have a slender endopod, with the ischiomerus and basis fused, but distinctly demarcated. The ischiomerus is sparsely setose medially, with a single large fusiform seta at about 0.5 of the combined segment length, about 0.25 mm in length, 5.75 longer than wide. A small arthrobranch, with rudimentary lamellae, is present. The fourth thoracic sternite has a small triangular median process, the fifth has a pair of long acute submedian teeth, other segments are unarmed. The first pereiopod is slender, with the chela about 0.55 of the carpus length. The fingers are about 1.5 times the palm length, deeply subspatulate with strongly denticulate lateral cutting edges. The tip of the dactyl bears a single stout tooth, with a thin, feebly crenulate transparent lamella medially. The tip of the fixed finger bears a pair of similar teeth with an acute lamellar process medially. The ambulatory propods are moderately slender, the third propod is about 16.5 times longer than wide, with a pair of long distovental spines and five smaller ventral spines. The dactylus is about 0.23 of the propod length, compressed, with unguis not distinctly demarcated, about 4.2 times longer than proximal width, with a long and a short seta at about 0.5 of the dorsal margin length and a pair of distolateral sensory setae. The first pleopod has the endopod about 0.9 of the exopod length, about 5.8 times longer than proximal width, slightly expanded distally, proximal fourth of medial margin with four long sparsely setulose setae, central half with six fine simple setae, with 11 short plumose setae round the distal margin. The endopod of the second pleopod bears appendices at about 0.5 of the medial margin length, the appendix masculina distinctly exceeding the appendix interna but not the tip of the endopod. The corpus is subcylindrical about 4.5 times longer than wide, 0.33 of the endopod length, with three stout spines distally, the longest spine almost subequal to the corpus length, finely serrulate along the lateral margins, with two distolateral, and three distomedial simple setae.

The holotype specimen lacks all mouthparts, so it cannot be determined if the unusual fusiform setae on the ischiomerus of the third maxillipeds of the Lizard

Island specimen were present or not. However, similar setae, which have not been reported in any other pontoniine shrimp, were noted as occurring on the distoventral merus of the second pereiopods. The exact similarity of left and right maxillipeds in the Lizard Island specimen, supports the view that their presence is a normal feature and not due to damage or injury.

The specimens of *P. denticulatus* reported from

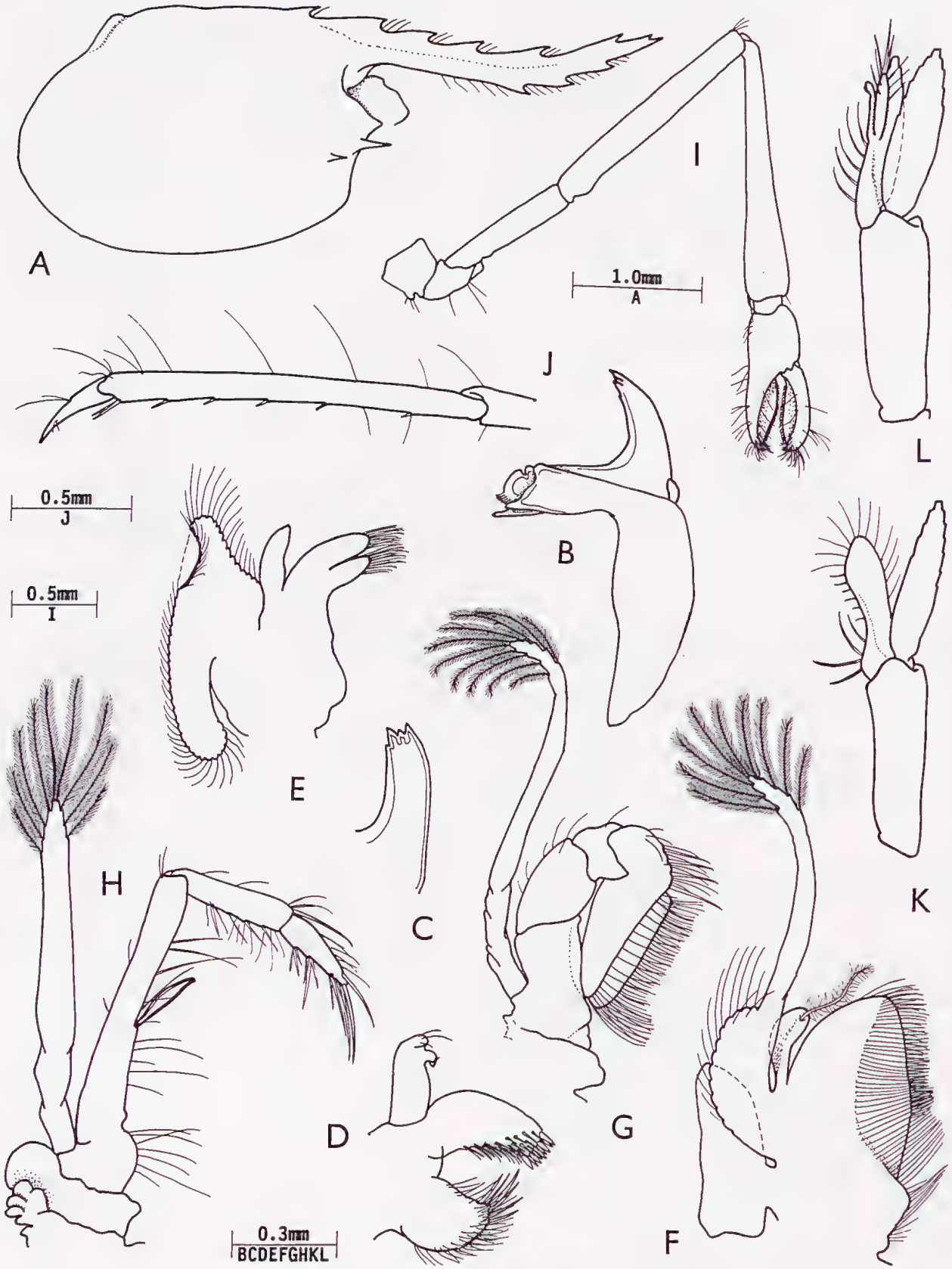

Fig.12. *Periclimenes denticulatus* Nobili, Lizard Island, male. A, carapace and rostrum; B, mandible (right); C, same, incisor process; D, maxillula; E, maxilla; F, first maxilliped; G, second maxilliped; H, third maxilliped; I, first pereiopod; J, third pereiopod, propod and dactyl; K, first pleopod; L, second pleopod.

Eniwetak Atoll, (Devaney & Bruce, 1987) have also been re-examined and found to be closely similar to the present specimen, except that one of the third maxillipeds bears two fusiform setae and the other three. As in the Lizard Island specimen, these setae are about 0.20 to 0.24 mm long. The distolateral merus of the third maxilliped also bears three small mobile spines. The two specimens, which are macerated, are in poor condition (male CL 2.1 mm, R. 1+7/3; female CL 2.1 mm, R. 1+7/3). The female has both second pereiopods, which are similar, subequal, with three strong acute spines on the distal margin of the carpus, with three distoventral spines and a preterminal distomedial spine on the merus. The merus does not show any of the fusiform setae as found in the holotype, but these were noted in that specimen as very easily detached. The distoventral angle of the merus is unarmed. The chela is slender, with the palm subcylindrical, feebly compressed, smooth, about 0.18 of the carpus length, 4.6 times longer than wide; the fingers are slender, with acute moderately hooked tips. The dactylus is about 8.5 times longer than its proximal width, with a small proximal fossa medially, the distal cutting edge entire, the proximal cutting edge with seven to eight low teeth, without any trace of sound-

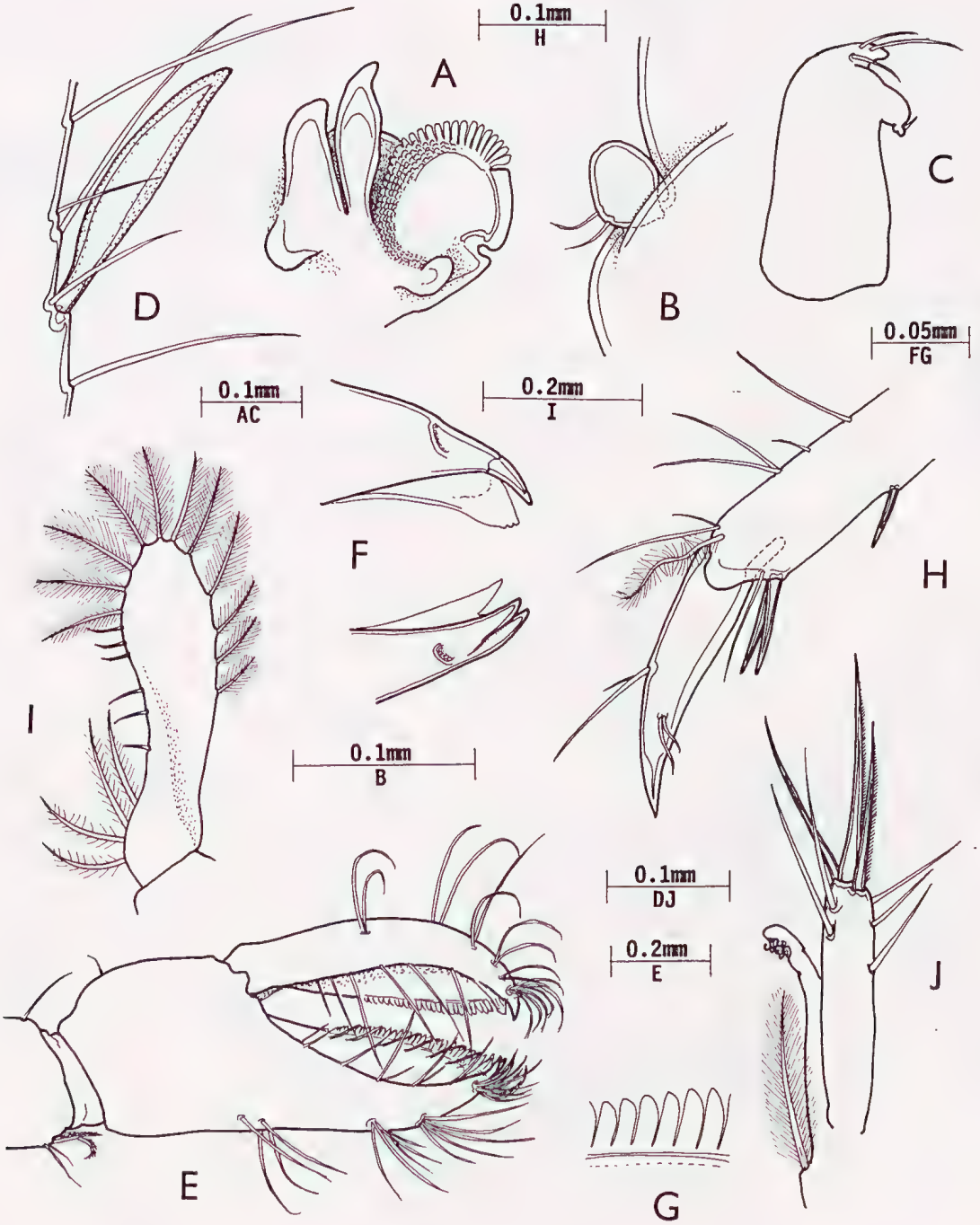

Fig.13. *Periclimenes denticulatus* Nobili, Lizard Island. A, mandible, right molar process; B, same, palp; C, maxillula, palp; D, third maxilliped, ischiomeral seta; E, first pereiopod, chela; F, same, tips of fingers, dactyl above; G, same, fixed finger, central cutting edge; H, third pereiopod; I, first pleopod, endopod; J, second pleopod, appendix masculina and appendix interna.

producing fossa. The fixed finger is similar. The single male second pereiopod is also similar but the merus bears only two distoventral teeth, instead of three.

Comparison of the Lizard Island specimen with the holotype of *P. denticulatus*, and with the specimens of *P. denticulatus* from Eniwetak Atoll, leaves little doubt as to its identity, despite the lack of second pereiopods, and represents a considerable extension to the known range of the species as well as an addition to the Australian fauna. *Periclimenes denticulatus* appears to be a naturally rare species, although two of its closest relatives, *P. spiniferus* de Man, occurring throughout most of the Indo-west Pacific region, and *P. petitthouarsii* (Audouin) in the western Indian Ocean, Red Sea, Persian Gulf region, are amongst the commonest coral reef shrimps. *Periclimenes denticulatus* shares with these two species, and also with *P. sibogae* Holthuis, the presence of a median tooth on the fourth thoracic sternite and a pair of very acute submedian teeth on the fifth, with long, slender first pereiopods with strongly subspatulate chelae, with pectinate lateral cutting edges to the fingers, elongate second pereiopods, similar or dissimilar, fingers with or without sound-producing fossae, and ambulatory pereiopods with simple dactyls.

Distribution. Type locality – Gatavake, Mangareva Atoll, Gambier Islands. Also known from Arno and Enewetak Atolls, Marshall Islands; Raroia Atoll, Tuamotu Islands; and from the northern South China sea. Not previously reported from Australian waters.

Periclimenes platycheles Holthuis, 1952

Fig.15

Restricted synonyny

Periclimenes (Harpilius) platycheles Holthuis, 1952: 85-87, fig.33.–Miyake & Fujino, 1968: 409-410, fig.3c-f.
Periclimenes platycheles.–Bruce, 1983 : 196.

Material examined. (i) 1 male, 1 ovig. female, stn Qld-278, between Palfrey and South Islands, Lizard Island, 21 m, trap, 29-30 Jan. 1989, coll. J.K. Lowry, S.J. Keable, AM P39304. (ii) 1 female, with hemiarthrinid bopyrid, stn Qld-142, off Eagle Island, Lizard Island, 9 m, trap, 13-14 Jan. 1989, coll. J.K. Lowry, AM P39292.

Remarks. The species has been previous reported

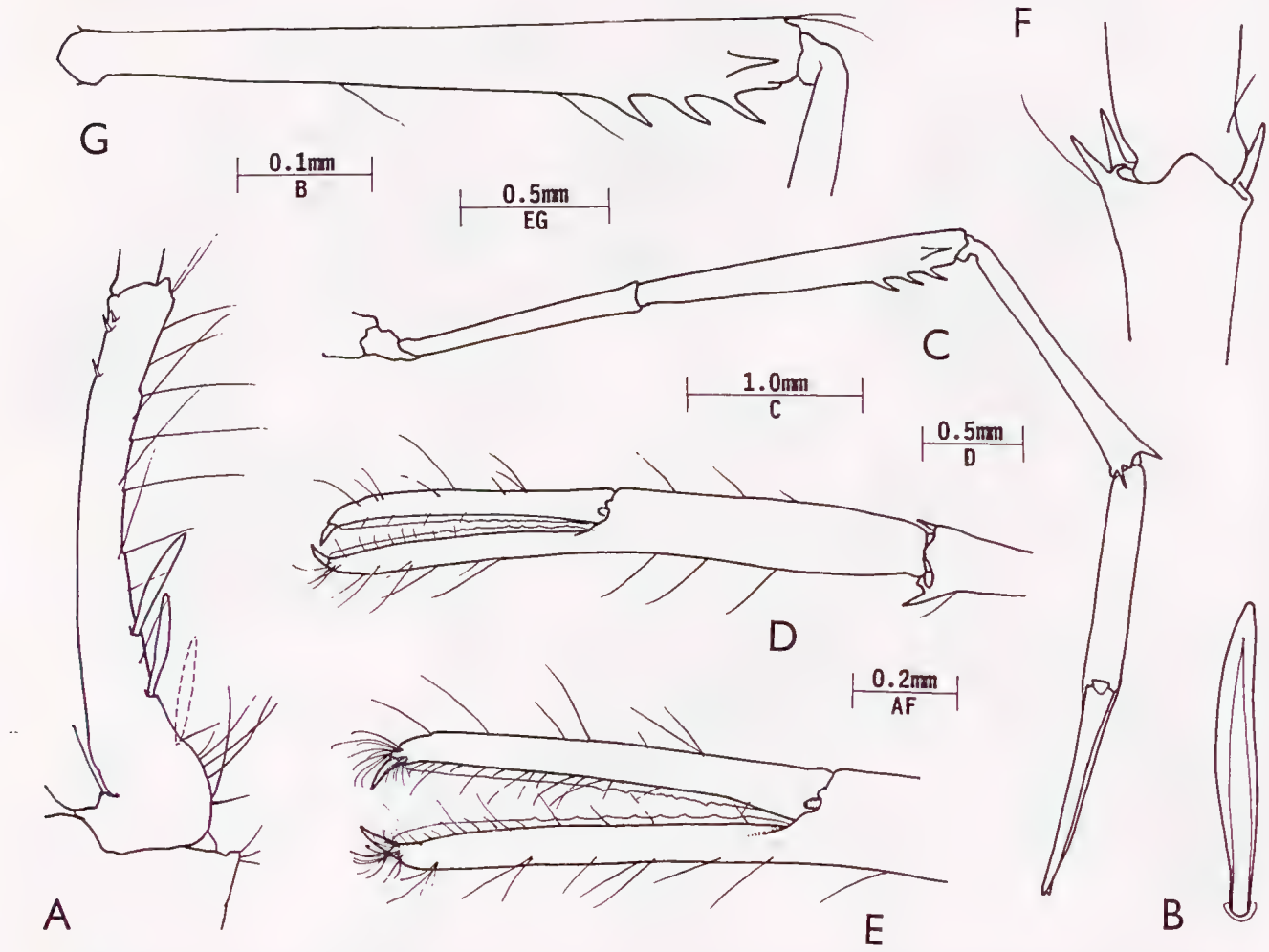

Fig.14. *Periclimenes denticulatus* Nobili, Enewetak Atoll, female. A, third maxilliped, ischiomeral-basal region of endopod; B, same, medial fusiform seta; C, second pereiopod; D, same, chela; E, same, fingers; F, same, carpopropodal joint; G, same, merus.

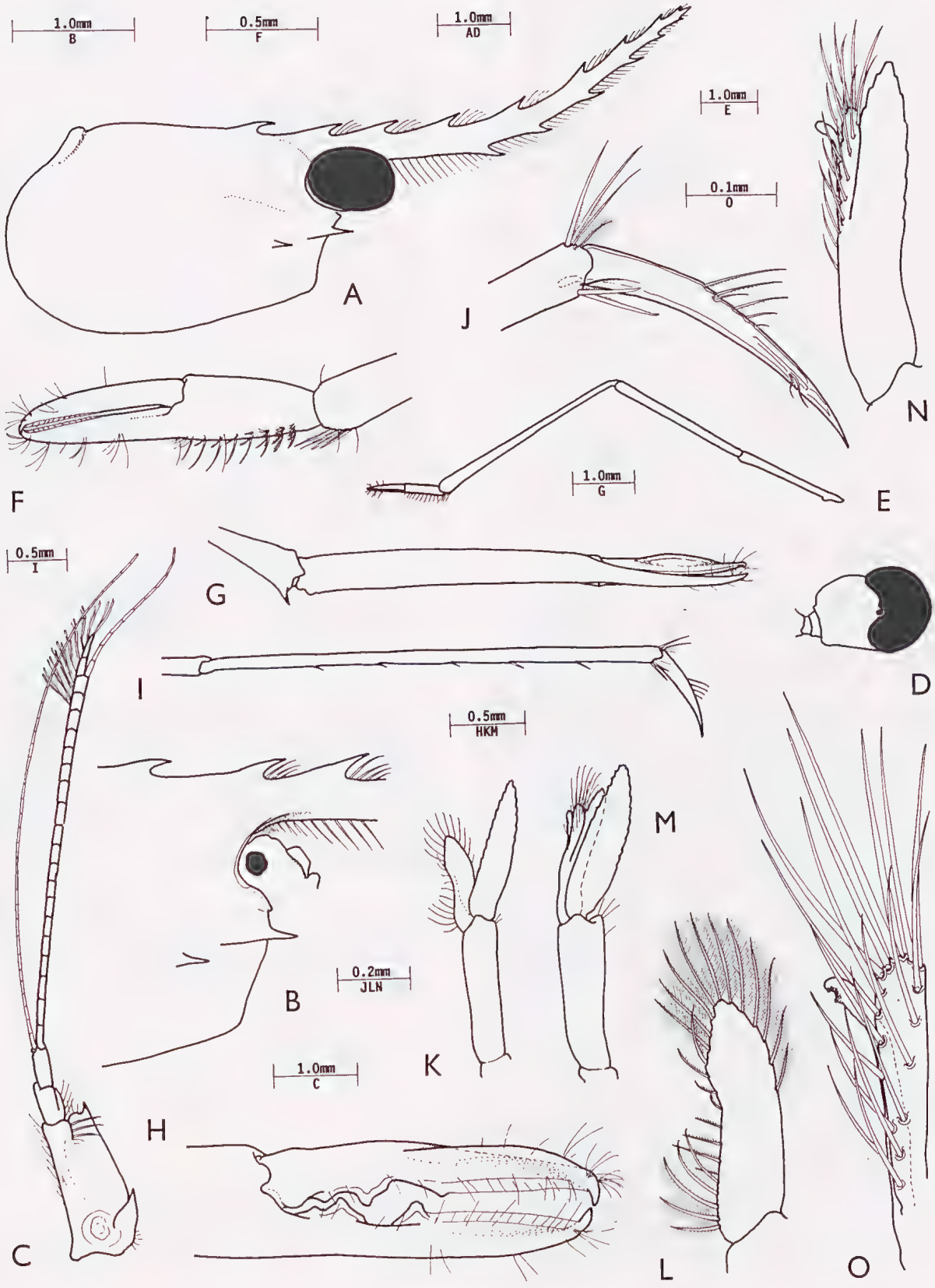

Fig.15. *Periclimenes platycheles* Holthuis, 1952, Lizard Island. A, carapace and rostrum; B, same, orbital region; C, antennule; D, eye; E, first pereiopod; F, same, chela; G, second pereiopod, chela; H, same, fingers; I, third pereiopod, propod and dactyl; J, same, distal propod and dactyl; K, first pleopod; L, same, endopod; M, second pleopod; N, same, endopod; O, same, appendix masculina and appendix interna; A-F, K-O, male; G,H, female; I,J?

from Lizard Island, from 14 m, by Bruce (1983). The present specimens agree closely with the original description. The male specimen, CL 3.3 mm, has the rostrum distinctly up-curved distally, with a dentition of 1+8/6. Both female specimens, CLs 3.5, 2.6 mm, have a dentition of 1+8/5. The type material had only 1 + 6/4 (ovig. female) and 1+6/6. The rostrum is about 1.75 times the carapace length. The inferior orbital angle is slightly produced, with a small ventral inner flange, the dorsal border is convex. The antennal spine is at a much lower level than the inferior orbital angle, which it far exceeds, and is broad, with a distinct carina laterally. The antennular peduncle is as previously described, with an acute tooth ventrally at the middle of the medial margin of the proximal segment. The upper flagellum has the rami fused for the 19 proximal segments in the male specimen, with the shorter flagellum consisting of only two short segments, and the longer flagellum of ten very slender segments. The stout upper flagellum, which is 1.5 times the carapace length, contrasts strongly with the lower flagellum, which is slightly longer and very slender, with about 35 poorly demarcated segments. About nine groups of aesthetascs are present distally. The eye has a large globular cornea, the diameter equal to about one third of the carapace length, with a distinct dorsal accessory pigment spot. The ophthalmic somite is without a bec ocellaire. The fourth thoracic sternite is armed with a slender finger-like median process and the fifth bears a transverse posterior ridge, with a small median notch. The third sternite is broad and the third maxilliped bears a vestigial arthrobranch with three rudimentary lamellae. The first pereiopod appears more slender than in Holthuis' illustrations (fig.33c), with the carpus about 2.75 times the chela length and distinctly longer than the merus. The fingers are about 1.2 times the palm length, slender, with short hooked tips, the cutting edges are sharp over the distal halves of the finger lengths and entire. They do not closely resemble those of *P. petitthouarsi* and *P. spiniferus*, as reported by Holthuis. The chela in Holthuis' figure appears quite distinct from that of *P. sibogae* (fig.28c), which is also closely similar to that of *P. petitthouarsi* and *P. spiniferus*, with the fingers much broader, far longer than the palm and with pectinate cutting edges. The male specimen has both pereiopods in an early stage of regeneration, the associated female has only a single second pereiopod preserved. The palm of the chela is slender, suboval in section, about 6.5 times longer than wide, twice the length of the fingers. The dactyl is slender, with a strongly hooked tip, the distal half of the cutting edge sharp, entire, with the proximal half bearing a small distal tooth, separated by a deep notch from a large irregular central tooth, with a smaller tooth proximally; the distomedial aspect of the dactyl bears a distinct flange. The fixed finger is similar, without a flange, but the distal tooth is larger, opposing into the large dactylar diastema and separated from the central tooth by a broad deep notch. The carpus bears one well-developed acute distal spine, with a subacute lobe dorsomedially. The ambulatory pereiopods are slender, with the propod about 25 times longer than wide, with a pair of long distoventral spines, finely pectinate proximodorsally, with about five shorter single spines ventrally. The dactyl is about 0.21 of the propod length, slender, curved, about 8.5 times longer than the proximal width, with an obscurely demarcated unguis, about 0.5 of the corpus length. The penultimate fourth of the dorsal border of the corpus bears a longitudinal row of five setae, of decreasing size distally, with the proximal ventral margins finely setulose. The male first pleopod has the basipodite about 4.0 times longer than wide, with the endopod about 0.7 of the basipodite length, 3.75 longer than the proximal width, slightly expanded distally, without a medial accessory lobule, the proximal fourth of the medial margin with five long coarsely setulose setae, the central half with seven serrulate spiniform setae, the distal medial and lateral margins having 12 short plumose setae. The second pleopod has the basipodite about 3.2 times longer than its distal width, subequal to the first basipodite length. The endopod is about 0.9 of the basipodite length, 1.5 times the first endopod length, with the appendices about 0.5 of the median margin length. The corpus of the appendix masculina is about 5.0 times longer than its distal width, 0.35 of the endopod length, falling far short of the tip of the endopod, with a longitudinal row of seven ventral spines, a similar row of seven medial spines and a group of five longer distal spines, all simple, non-setulose. The appendix interna is slender, subequal to the appendix masculina, feebly cincinnulate.

Parasites. The specimen from stn Qld-142 had a lateral abdominal hemiarthrinid parasite, *Metaphryxus intutus* Bruce, (Isopoda, Bopyridae), an association that represents a new host record. The parasite was attached, in typical fashion, to the left side of the host's abdomen, raising a small lateral flange on the lateral aspect of the first segment.

Distribution. Type locality – Fau Island, Gebe Island, Indonesia, 31 m. Also previously reported from Atiationin, Irian Jaya (paratype) (57 m); Palau, Caroline Islands, and Lizard Island, Queensland.

Periclimenes agag Kemp, 1922

Fig.16

Restricted synonymy

Periclimenes (Ancylocaris) agag Kemp, 1922: 197-201, figs 47-50, pl.7 fig.9.–Gurney, 1938: 16.
Periclimenes (Harpilius) agag.–Ledoyer, 1984: 27-28.

Material examined. (i) 1 male, 1 female, stn Qld-136, Coconut Beach, Lizard Island, 17 m, clean sand, trap, 11-12 Jan. 1989, coll. J.K. Lowry and S.J. Keable, AM P39288; (ii) 1 male, stn Qld-143, near Eagle Island, Lizard Island, 12 m, rubble and sand, trap, 13-14 Jan. 1989, coll. J.K. Lowry and S.J. Keable, AM P39297; (iii) 11 specimens, stn Qld-202, southern end of Mrs

Watson's Bay, Lizard Island, 1 m, mangrove creek, trap, 23-24 Jan. 1989, coll. J.K. Lowry, S.J. Keable, AM P39297.

Remarks. The specimens correspond well with the description provided by Kemp (1922). The rostrum is slender, distinctly exceeds the carapace length and the

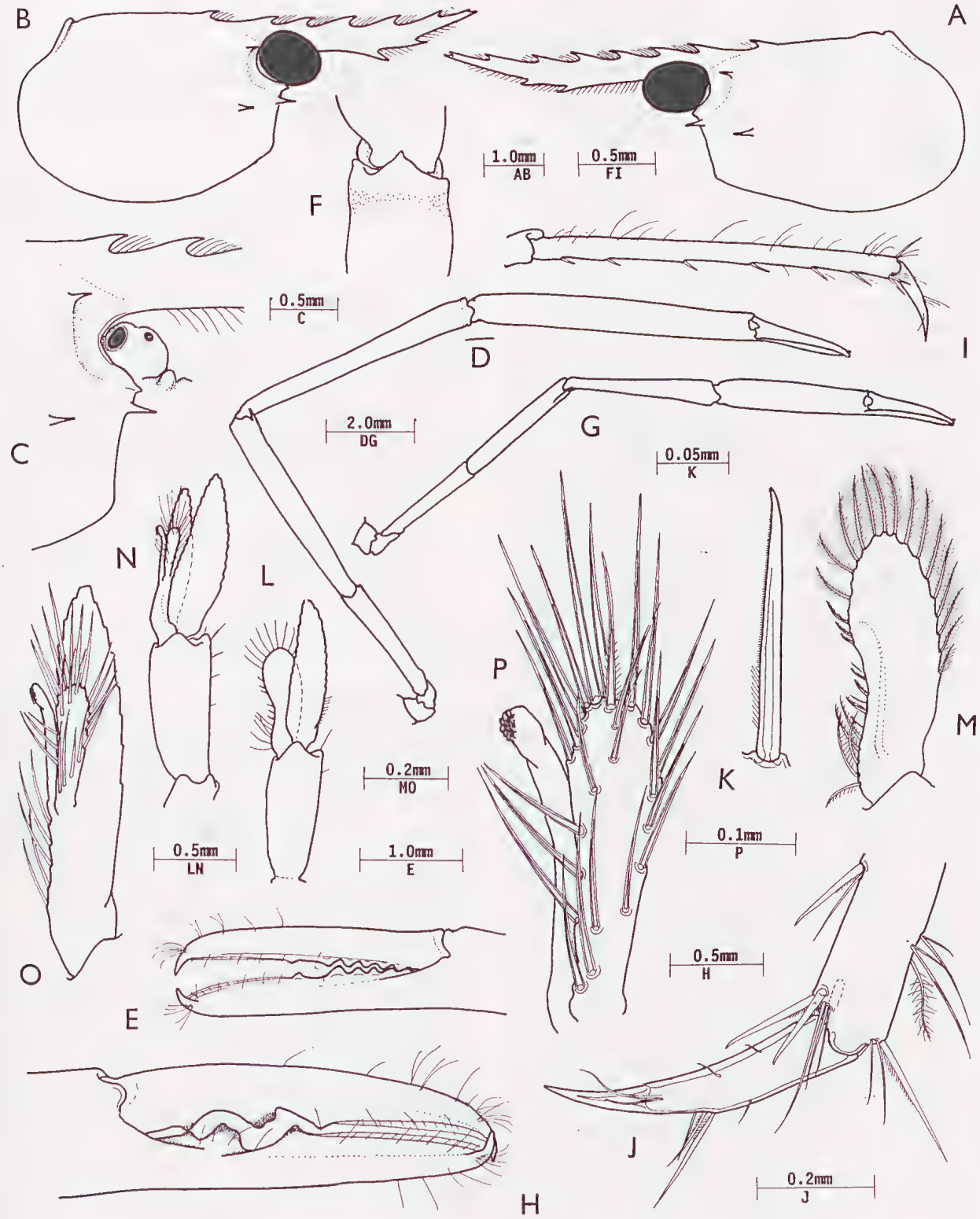

Fig.16. *Periclimenes agag* Kemp, 1922, Lizard Island. A,B, carapace and rostrum, lateral; C, same, orbital region; D, second pereiopod; E, same, fingers; F, same, carpopropodal joint, dorsal; G, second pereiopod; H, same, fingers; I, third pereiopod, propod and dactyl; J, same, distal propod and dactyl; K, same, distoventral propodal spine; L, first pleopod; M, same, endopod; N, second pleopod; O, same, endopod; P, same, appendix masculina and appendix interna. A,D,E,F,I-P, male; B,C,G,H, ovigerous female.

tip of the scaphocerite, and is slightly longer in the male than in the female, with a dentition of 1+6-7/2-3, except for a specimen from Qld-202, the largest male specimen, CL 3.4 mm, which is unusual in having two epigastric spines situated close together, separated by a large gap from the rest of the dorsal rostral teeth. The supraorbital spines are well developed and a lateral orbital ridge is feebly indicated. The inferior orbital angle is slightly produced with a small ventral inner flange. The antennal spine is slender, marginal and exceeds the inferior orbital angle. In Kemp's illustration (fig.47), the antennal spine appears more robust and distinctly postmarginal, in contrast to the other species in his *Periclimenes grandis* group. The hepatic spine is at a slightly lower level, slightly posterior to the level of the supraorbital spine. The merus of the first pereiopods is about twice the length of the chela. The second pereiopods are very well developed, long and slender. In the male, the scaphocerite is exceeded by the distal third of the merus. The carpus has a small subacute tooth on the inner side and the ischium bears a small distoventral tubercle in large male specimens. In the male, the chela is about 1.5 times the carpus length and in females, about 1.6 times. Most of the 11 specimens from Qld-202 have all pereiopods detached and only few second pereiopods preserved. The male from Qld-143 has both preserved and the pair from Qld-136 only lacks one second pereiopod from the male. The fingers are about 0.36 of the palm length in the male, 0.55 in the female. In the male, a low, subacute tooth is present at about the middle of the cutting edge length, separated by a shallow gap from a proximal series of five low blunt teeth. The distal cutting edge is entire and the tip strongly hooked. In the single pereiopod of the female specimen the teeth are much more strongly developed and fewer in number, with more deeply developed interspaces. The third pereiopod is moderately slender, with the propod about 4.5 times the dactyl length, 14.5 times longer than wide, with a pair of long distoventral spines and six well-developed ventral spines, and the fifth pereiopod distinctly exceeds the scaphocerite. The dactylus is compressed, curved, simple, with a feebly demarcated unguis, 5.0 times longer than the proximal width, a longitudinal group of three slender setae at about 0.5 of the dorsal margin length, the two larger setae being finely setulose proximoventrally, the corpus with a pair of slender setae distolaterally and a few short ventral setae. The male first pleopod has the basicerite 2.5 times longer than wide, with the endopod about 0.8 of the basipodite length, 3.1 times longer than distal width, slightly expanded distally, medial margin concave, without accessory lobule, proximal fourth with four coarsely setulose setae, central half with about seven serrulate spines, distal and lateral margin with 15 short plumose setae. Second pleopod with basipodite 2.4 times longer than wide, 1.1 times first basipodite length; endopod 5.5 times longer than wide, subequal to basipodite length, with appendices at 2.4 of medial margin length, appendix masculina with corpus subcylindrical, slightly swollen distally, 3.4 times longer than distal width, reaching to point at 0.75 of endopod length, with ten ventromedial, four distoventral, eight ventrolateral and two to three distal spines, one feebly setulose proximally, others simple; appendix interna, slender, subequal to appendix masculina with few distal cincinnuli only.

Distribution. Type locality – Port Blair, Andaman Islands, (7-15 m). Also reported from the Red Sea and New Caledonia. Not previously reported from Australian waters.

Periclimenes amboinensis (De Man, 1888)

Figs 17, 18

Restricted synonymy

Anchistia amboinensis De Man, 1888: 546, pl. 22a fig.2.
Periclimenes amboinensis.–Borradaile, 1898: 385.–Bruce, 1983a: 874-875, figs 1-3, 7e.
Periclimenes (Corniger) amboinensis.–Borradaile, 1917: 366.
Periclimenes (Ancylocaris) amboinensis.–Kemp, 1922: 172.
Periclimenes (Harpilius) amboinensis.–Holthuis, 1952: 10.

Material examined. 1 male, 1 juvenile, stn 26.1.0, Marx Reef, 15°12'S 145°37'E, 3.0 m, 21 July 1988, coll. K. Fabricius, NTM Cr.006835.

Host. *Himerometra magnipinna* A.H. Clark (Echinodermata, Crinoidea).

Remarks. The larger specimen is remarkable in that the cornea of the left eye is distinctly conoidally produced while that of the right eye is smoothly rounded. The conoidal corneal process is a character of major taxonomic importance, and its presence was at one time used as a basis for the distinction of the subgenus *Corniger* by Borradaile (1915). Loss or non-development of this process of both eyes would probably have resulted in the description of a new species.

The male specimen otherwise conforms closely to the data provided from Indonesian material by Bruce (1983a). The rostrum slightly exceeds the antennular peduncle and has six dorsal teeth and one small ventral tooth. The epistomal horns are well developed. The first four thoracic sternites are broad, all unarmed, the fifth narrow, and the following sternites relatively broad, also unarmed. The proximal segment of the antennular peduncle has a strong ventromedial tooth, the distoventral angle bears a single acute tooth only. The upper flagellum is biramous with the four proximal segments fused, the short ramus with only two free segments and the longer with ten slender segments; about nine groups of aesthetascs are present. The lower flagellum has about 14 slender segments. The scaphocerite distinctly exceeds the antennular peduncle, is 3.0 times longer than wide, with a small distolateral tooth far exceeded by the distal margin of the lamella. The mouthparts are as previously described, the broadened

incisor processes of the mandibles having eight acute teeth on each side. The chela of the first pereiopod is slightly bowed, with slender fingers, about 0.8 of palm length, with entire sharp cutting edges distolaterally; the fixed finger is deeply channelled proximally and both fingers are very densely setose laterally. The chelae of

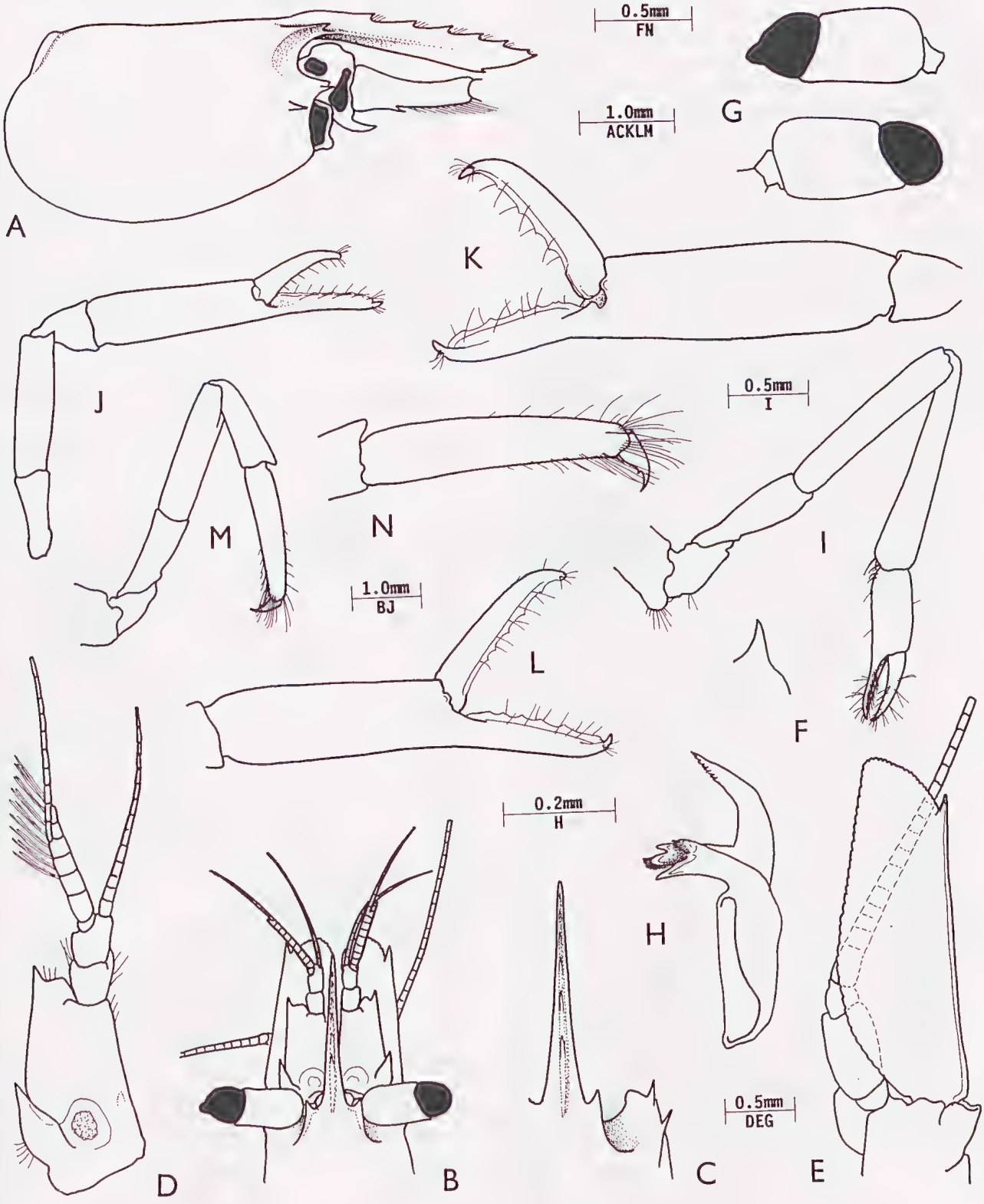

Fig.17. *Periclimenes amboinensis* (De Man), Marx Reef, male: A, carapace and rostrum, lateral right antennal peduncles removed, showing right epistomal horn; B, anterior carapace, rostrum, antennal peduncles, dorsal; C, right orbital region, dorsal; D, antennule; E, antenna; F, right epistomal horn, dorsal; G, eyes, (upper, left; lower, right), dorsal; H, mandible; I, first pereiopod; J, second pereiopod, major; K, same, chela; L, minor second pereiopod, chela; M, third pereiopod; N, same, propod and dactyl.

the second pereiopods are slightly unequal, similar, the major chela about 1.2 times the carapace length, palm 3.2 times longer than wide. The merus has a strong acute distoventral angle. The ambulatory pereiopods are robust, with the distoventral angle of the merus unarmed. The propod is about 5.0 times longer than wide, slightly tapering distally, with a pair of short, slender distoventral spines and three small isolated ventral spines on the distal fourth, all largely obscured by groups of long, relatively stout simple setae. The dactyl is curved, about 0.2 of the propod length, with the unguis clearly demarcated, about 0.68 of the corpus length; corpus compressed with a small erect acute distoventral tooth, ventral border sinuous, with three long sensory setae distolaterally. The endopod of the first pleopod is 3.5 times longer than broad, distally rounded, without a median accessory lobule, the proximal medial border bearing five slender simple spines and the distolateral margin with four short plumose setae. The second pleopod has the appendix interna distinctly exceeding the appendix masculina. The corpus of the appendix masculina is about 0.28 times longer than distal width, with five spinulate ventral setae, of increasing length distally, and two long stout spinulate distal setae, the longer subequal to the corpus length. The caudal fan is normal, the telson with small dorsal spines at about 0.5 and 0.75 of its length. The lateral posterior spines are longer than the dorsal spines, and the submedian spines are finely setulose.

The juvenile specimen has a CL of 1.15 mm, with the carapace and rostrum 2.45 mm. The rostrum has three small acute dorsal teeth and a single small ventral tooth. The cornea is hemispherical, about 0.82 of the stalk length, 0.33 of the carapace length, quite without any conoidal process. The second pereiopods are subequal, with the chela subequal to the carapace length, fingers about 0.55 of palm length, palm 2.5 times longer than wide. The ambulatory dactyl is similar to that of the adult. The propod is also similar, with two slender distal spines and two small single ventral spines, but distinctly less setose, with only a few broad, rather spiniform setae.

Distribution. Type locality – Ambon, Indonesia.

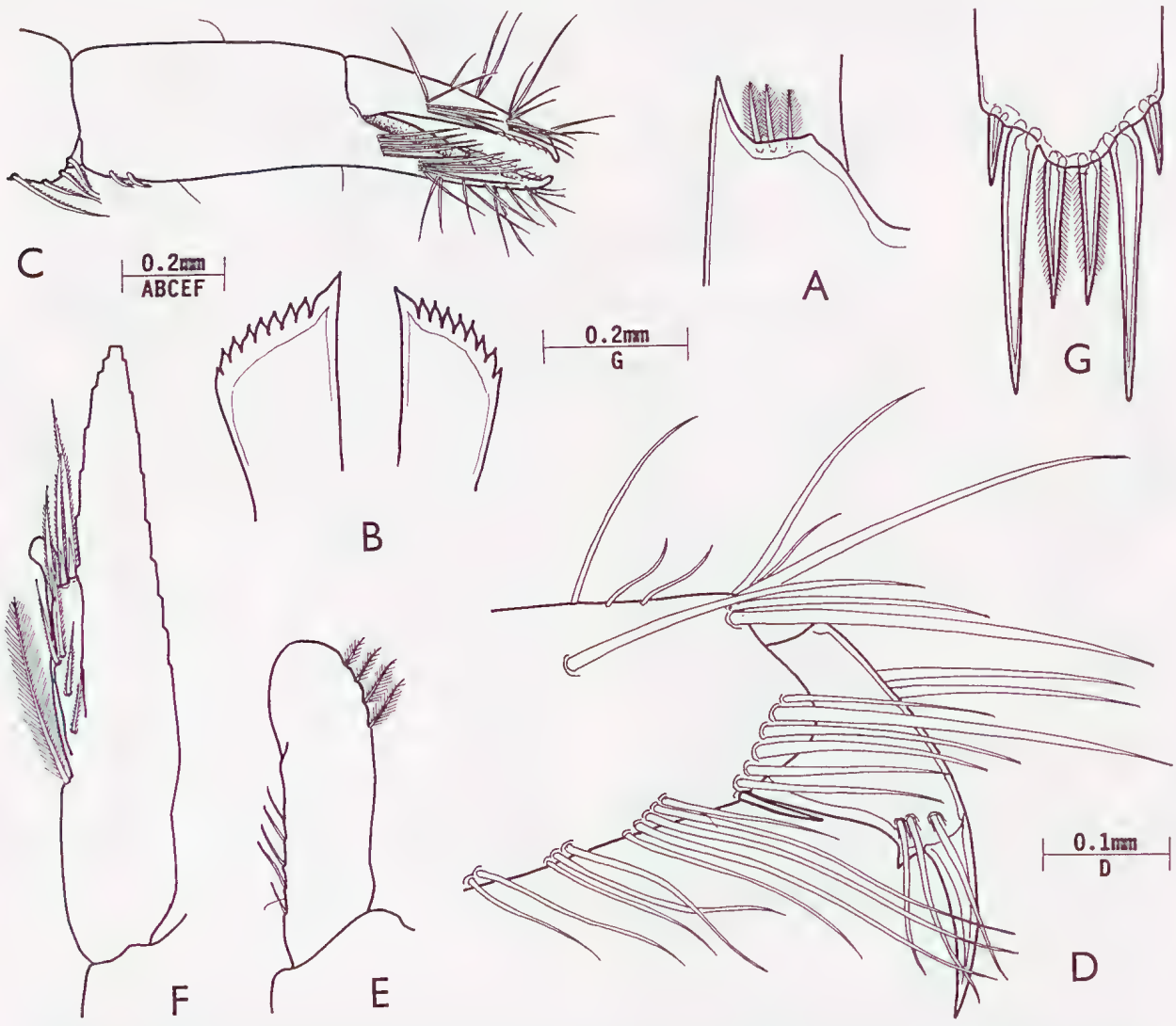

Fig.18. *Periclimenes amboinensis* (De Man), Marx Reef, male, A, proximal segment of antennular peduncle, distolateral angle; B, mandibles, incisor processes; C, first pereiopod, chela; D, third pereiopod, distal propod and dactyl, lateral, (many medial setae omitted); E, first pleopod, endopod; F, second pleopod, endopod.

Also known from Marsegu Island, Ceram and Banda, Indonesia, the Great Barrier Reef, New Caledonia and the Marshall Islands.

Periclimenes attenuatus Bruce, 1971

Fig.19

Restricted synonymy

Periclimenes attenuatus Bruce, 1971: 533-542, figs 1-5.–Bruce, 1983: 206.–Bruce, 1983a: 879.

Material examined. 1 male, 1 ovig. female, 42/1/1, Rib Reef, 18°29'S 147°53'E, 10 m, north reef front, 4 Nov. 1989, coll. K. Fabricius, NTM Cr.006836.

Host. *Comaster multifidus* (J. Müller, 1841) (Echinodermata: Crinoidea).

Remarks. The female specimen has a carapace length of 2.8 mm and is the first ovigerous female reported. The type material was considered to be possibly immature, a finding that is confirmed by the present specimen, which is considerably more robust, with a much more strongly developed major second pereiopod. The major second pereiopod is lacking in the associated male. The present female differs from the holotype in having a rostral dentition of 4/0, with a small preterminal tooth, instead of 3/0. In both specimens the cornea is distinctly conoidally produced, whereas it was described as globular in the type specimens, although figured as very feebly produced. The chela of the female major second pereiopod has the palm subcylindrical, feebly compressed, slightly swollen proximally, about 3.2 times longer than proximal width, with the fingers about 0.37 of palm length, the dactyl about 3.75 times longer than proximal depth, rather swollen proximally, with feeble lateral flange, the cutting edge bears a much larger, broad, blunt tooth proximally, fitting into a large fossa on the fixed finger, with a ventrolateral flange laterally; the distal cutting edge is sinuous, proximally entire, distally finely serrate, with a large curved blunt tip; the fixed finger has two large teeth proximally, the most proximal low, irregularly blunt, the distal tooth, slender, strongly produced, blunt, fitting into a deep fossa on the dactylus, the distal cutting edge similar to the dactylus. The ova are numerous and small, about 0.45mm in length.

Periclimenes attenuatus has not been previously recorded in association with *Comaster multifidus*.

Distribution. Type locality – Burukuk Island, Duke of York Islands. Also known from Lizard Island, Queensland, and from Sawai, Seleman Bay, Seram, Indonesia.

Periclimenes laccadivensis (Alcock & Anderson, 1894)

Fig.20

Restricted synonymy

Palaemonella laccadivensis Alcock & Anderson, 1894: 157.–Rathbun, 1906: 925, pl.20 fig.2.
Palaemon (Brachycarpus) laccadivensis.–Alcock, 1901: 138 (*partim*).
Periclimenes (Periclimenes) laccadivensis.–Kemp, 1922: 153-154, figs 19-20.–Holthuis, 1952: 9.
Periclimenes laccadivensis.–Bruce, 1979: 225.

Material examined. 1 female, stn Slope 46, off Cape Freycinet, Tasmania, 40°20'S 148°37.70'E, 720 m, coarse shelly sand, R.V. *Franklin*, WHO1 epibenthic sled, 27 July 1986, coll. M.F. Gomon *et al.*, NMV J.15873.

Description. The single example is fairly complete, but lacks the major second pereiopod and some of the ambulatory pereiopods. The carapace (CL 4.2-mm) is slightly distorted, but the rostrum is complete, about 0.9 of the carapace length, slightly upcurved, distally slender and slightly exceeding the antennular peduncle but not the scaphocerite, with eight acute dorsal teeth, the first tooth postorbital in position, and with two similar ventral teeth at about 0.5 of the rostral length. Compared with Kemp's illustrations (fig.19), the hepatic spine appears distinctly longer and more robust. The epigastric spine is also present and distinct. The inferior orbital angle is moderately produced, blunt, with the antennal spine marginal, at a slightly lower level, well above the level of the hepatic spine. The eye has a well-developed globular cornea, well pigmented, without a dorsal accessory pigment spot. The stalk is about as wide as long dorsally, moderately compressed. The first pereiopod is slender, with the carpus about 1.5 times the chela length. The chela has slender, straight, simple fingers, slightly shorter than the palm length. Only the right second (minor) pereiopod is preserved. The carpus and merus are unarmed, the chela has the palm smooth, about 5.0 times longer than wide, 0.6 of the carapace length, with the fingers about 0.6 of the palm length, very feebly armed with minute teeth proximally. The ambulatory pereiopods are normal, one third and both fourth pereiopods are lacking. The third pereiopod has the dactyl about 0.18 of the propod length, about 3.8 times longer than deep, with a distinct unguis, about 3.8 times longer than wide, 0.45 of the corpus length; the corpus bears a slender acute distoventral tooth, about 0.25 of the unguis length. The propod is about 11.7 times longer than wide, with several groups of long setae distoventrally, but without any spines. The fifth pereiopod propod and dactyl are similar, but the propod has a single distoventral spine and a single ventral spine at about 0.70 of the propod length, the long setae are also more numerous, especially distolaterally. The thoracic sternites are moderately broad and unarmed, the fourth lacks a finger-like median process. The telson is

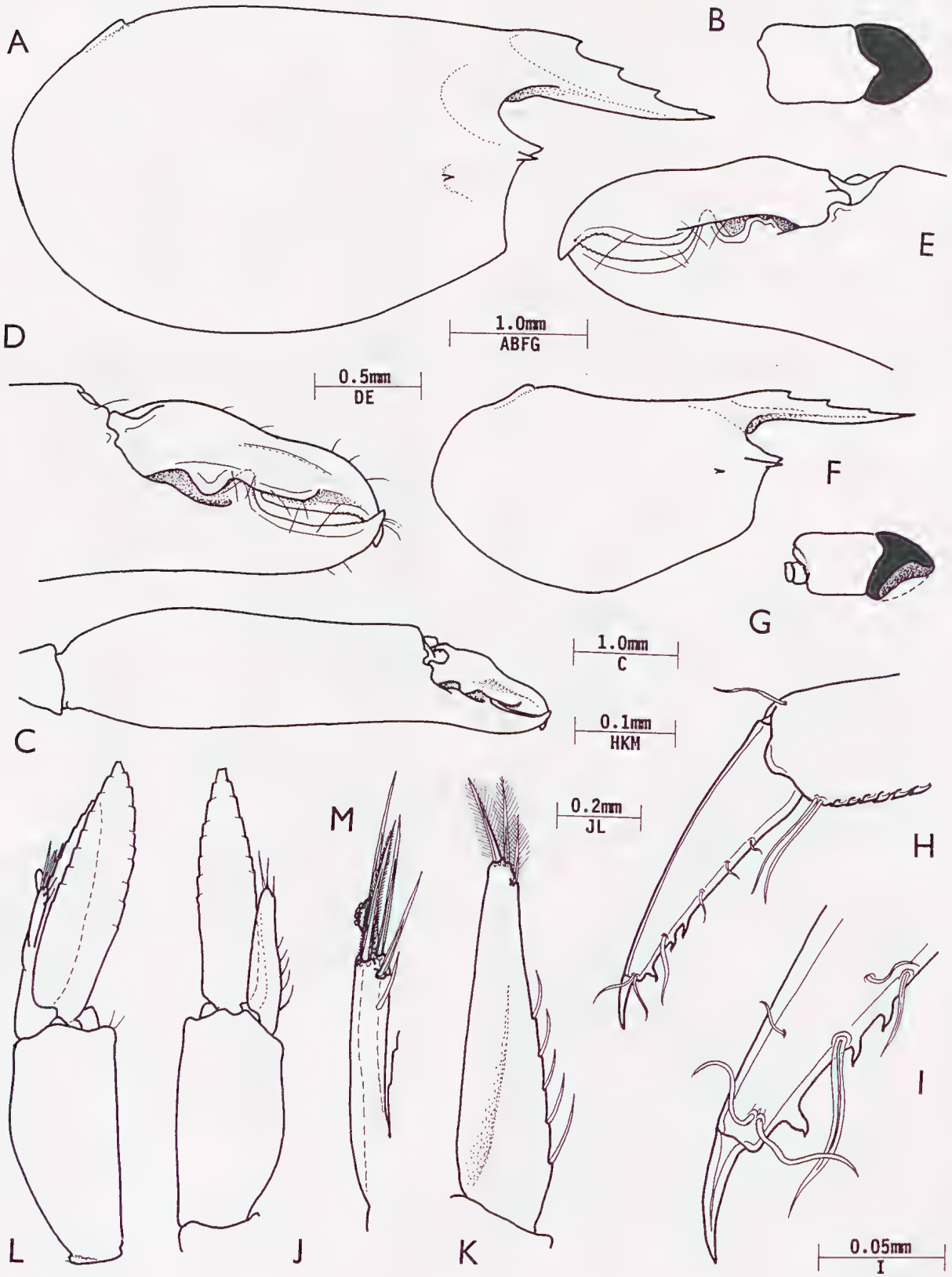

Fig.19. *Periclimenes attenuatus* Bruce, Rib Reef, Queensland. A, carapace and rostrum, lateral; B, eye; C, major second pereiopod chela; D, same, fingers, lateral; E, same, medial; F, carapace and rostrum, lateral; G, eye; H, third pereiopod, dactyl and distal propod; I, same, distal dactyl; J, first pleopod; K, same, endopod; L, second pleopod; M, same, appendix masculina and appendix interna. A-E, ovigerous female; F-M, ovigerous male.

about 1.1 times the length of the sixth abdominal segment, 4.15 times longer than broad, with dorsal spines well developed, slightly irregularly placed, about 0.45 and 0.72 of the telson length, sub-erect, larger than lateral posterior spines; posterior margin triangular, without acute median point, lateral spines subventral, intermediate spines about 9.0 times longer than wide, 0.2 of the telson length, submedian spines about 0.4 of intermediate spine length, robust, about 6.5 longer than wide, bilaterally setulose, with a single median spine exactly similar to the submedian spines. The uropods are normal, with the lateral margin of the exopod with a small acute distal tooth, with a larger mobile spine medially.

The present specimen of *P. laccadivensis* differs only slightly from the data provided by Kemp (1922). The rostrum is slightly longer, and has only one instead of two postrostral teeth. The antennal spine appears slightly less robust and the hepatic spine better developed. The telson is unusual in having seven posterior marginal spines, but minor abnormalities of spinulation are comparatively common in these spines. These abnormalities are usually conspicuously asymmetrical and the appearance of perfect symmetry, as in the present specimen, is most unusual. The present record is also the first report of *P. laccadivensis* from the southern hemisphere and represents a considerable extension of the known range of this species. It also indicates the occurrence of this species outside the boundaries generally accepted to the shallow water components of the Indo-west Pacific fauna. Despite the great extension in range and the minor morphological

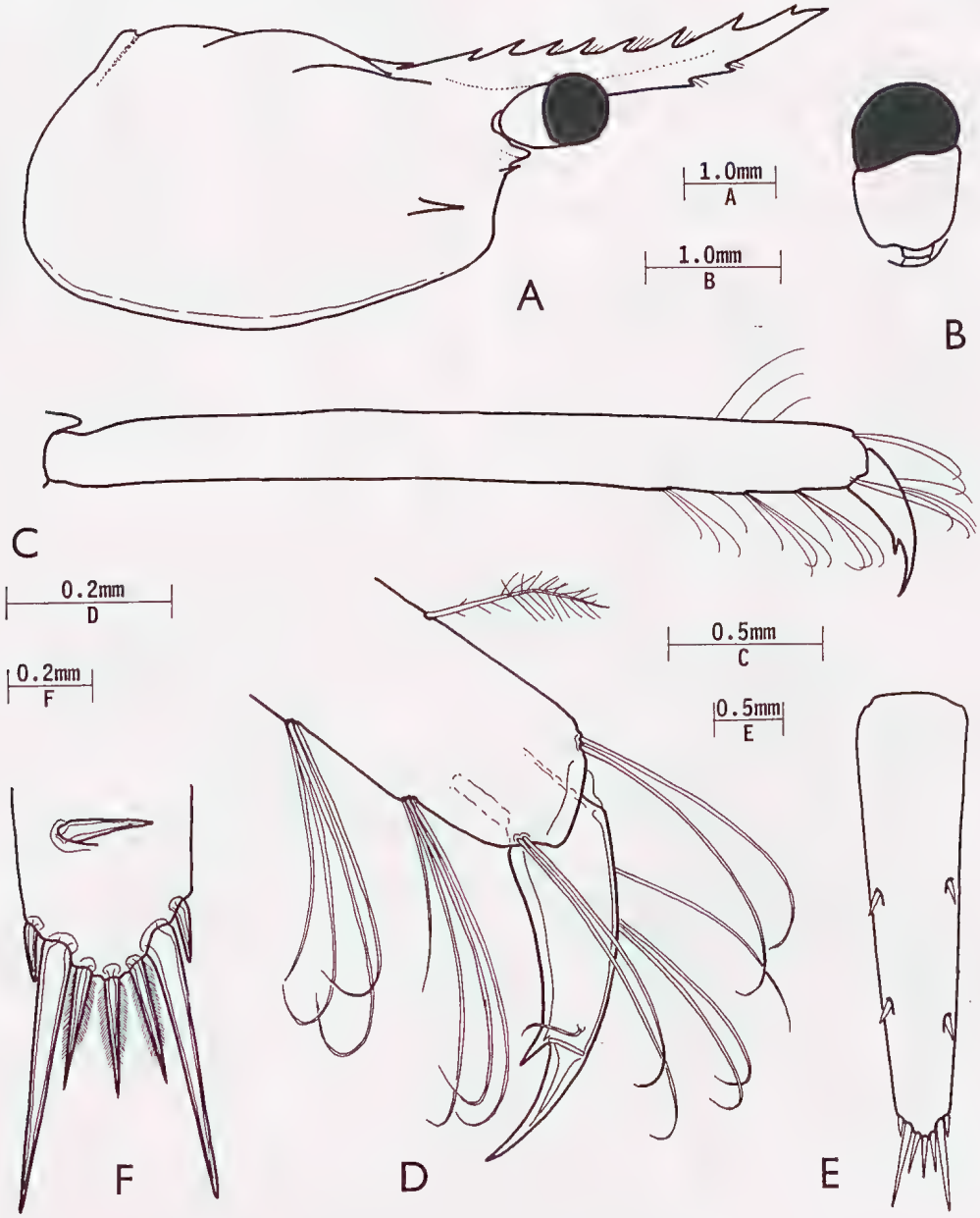

Fig.20. *Periclimenes laccadivensis* (Alcock & Anderson), Tasman Sea, female. A, carapace and rostrum, lateral; B, eye, dorsal; C, third pereiopod, propod and dactyl; D, same, dactyl and distal propod; E, telson; F, same, posterior spines; dorsal spine, inset.

differences, there is no adequate reason not to include this specimen under the name given.

Distribution. Type localities – Laccadive Sea, 10°47'45"N 72°40'20"E, 1285 m; 7°17'30"N 76°54'30"E, 786 m. Also reported from the South China Sea, 19°02'N 112°39'E, 274-289 m, and from Hawaii, off Kauai Island, 700-900 m. Not previously recorded from Australian waters.

"*Periclimenes consobrinus*" Balss, 1915

Fig.21

non *Harpilius consobrinus* De Man, 1902: 836-840, pl.26 fig.54.
Periclimenes consobrinus.–Balss, 1915: 27.

Material examined. NHMV unregistered - (i) 1 female, Yenbo; (ii) 1 male, Dahab; (iii) 1 female, Tor; (iv) 6 specimens, Ras Abu Somer.

Hosts. Not known, presumably *Acropora* spp.

Remarks. The examination of these specimens reported upon by Balss (1915) and collected by the '*Pola*' Expedition to the Red Sea, have failed to confirm the presence of *Periclimenes consobrinus* De Man in the Red Sea. The distinction of *P. consobrinus* from *P. lutescens* (Dana), treated as synonymous by Kemp (1922) and Holthuis (1952), was demonstrated by Bruce (1972) and confirmed, with further detail, by Holthuis (1981). Re-examination of Balss' specimens has recently shown that some of the specimens he reported as *P. consobrinus* are actually *P. lutescens*, first reported from the Red Sea by Nobili (1901) and then Tattersall (1921), as *Harpilius lutescens* and *H. depressus* respectively, but also include some other pontoniine shrimps. The results of this re-examination are summarised below and some further details included.

Specimen (i): *Philarius gerlachei* (Nobili, 1905), male, CL 4.2 mm. The single specimen lacks both second pereiopods, has a rostral dentition of 4/1, and has a broad blunt triangular median process on the fourth thoracic sternite. The propods of the ambulatory propods are stout, devoid of spines, with transverse rows of numerous simple setae distally. The dactyl is comparatively feeble, compressed, strongly curved, with a distinctly demarcated unguis, 3.0 times longer than the proximal width, 0.4 of the corpus length, about 2.0 times longer than the proximal width, which is only about 0.4 of the width of the distal end of the propod. The ventral margin of the corpus is concave, sharp and entire, without a distal accessory tooth. The dactyl is highly mobile, flexing about 90°, both dorsally and ventrally.

Specimen (ii): *Periclimenes lutescens* (Dana, 1852), male, CL 4.7 mm. The specimen has a rostral dentition of 7/2, with the first tooth just posterior the posterior margin of the orbital notch, the rostrum distinctly exceeding the antennular peduncle, by the portion beyond the sixth dorsal tooth, generally similar to the figure provided by Kemp (1922), but the antennal spine is distinctly less robust. The fourth thoracic sternite has a short finger-like median process on a feeble transverse ridge. The second pereiopod chela is about 2.3 times the carapace length, with the palm subcylindrical, slightly swollen proximally, about 3.0 times longer than the proximal depth, fingers slender, about 0.75 of palm length, dactyl 5.4 times longer than proximal depth, with strong blunt curved tip, proximal cutting edge with five low similar teeth, distal cutting edge entire, sharp; carpus about 0.4 of palm length, 2.0 times longer than distal width, slightly expanded distally with blunt lobes; merus with distoventral angle acute, distomedial angle bluntly produced; ischium, basis and coxa normal. The second maxilliped endopod has the narrow elongate dactylar segment forming a continuous straight medial margin with the inner edge of the propodal segment. The ambulatory pereiopods are stout, with the propod robust, compressed and without spines, with numerous long simple setae, arranged in four main transverse rows distolaterally. These largely obscure the dactyl, which is relatively feebly developed, its length about subequal to the distal width of the propod, its basal width about 0.45 of the distal propod width, strongly curved, compressed, with slender distinctly demarcated unguis, 3.75 times longer than proximal width 0.4 of corpus length, corpus about 1.8 times longer than proximal width, ventral margin sharp, feebly concave, unarmed. The endopod of the first pleopod is about 4.5 times longer than the proximal width, with the distal half slightly expanded medially, with ten short plumose setae along the proximal half of the medial margin, becoming more spinulose distally; the distal half of the medial margin bears five similar setae proximally, changing to few feebly plumose setae distally; the lateral margin bears 12 short plumose setae. The endopod of the second pleopod has appendices at about 0.4 of the medial margin length with the appendix masculina far exceeding the appendix interna, with the corpus subcylindrical, reaching to about 0.66 of the endopod length, with six short simple ventromedial spines, seven similar ventrolateral spines, and five longer simple distal spines. The appendix interna reaches to about 0.6 of the appendix masculina length and has few distal cincinnuli.

Specimen (iii): *Periclimenes lutescens* (Dana, 1852), female, CL 4.5 mm, with a rostral dentition of 7/2.

Specimens (iv): (a) *Periclimenes lutescens* (Dana, 1852), 2 ovig. females, CL 5.8, 6.7 mm. The larger specimen has a rostral dentition of 8/2, the smaller, 5/2, but with the distal portion missing. (b) *Philarius imperialis* (Kubo, 1940), 1 male?, CL 4.8 mm, with a rostral dentition of 9/1, with the first tooth situated on the carapace in an epigastric position and separated by a wider interval from the rest of the teeth; the carpus of the second pereiopod has two acute dorsal teeth. (The specimen appears to be provided with two left second pereiopods). *Periclimenes imperialis* has been previously reported from the Red Sea, from Elat, by

Fig.21. *Periclimenes lutescens* (Dana), Dahab, male. A, carapace and rostrum, lateral; B, anterior thoracic region, ventral; C, major second pereiopod, chela, lateral; D, third pereiopod (?), distal propod and dactyl; E, first pleopod, endopod; F, second pleopod, endopod; G, same, appendix masculina and appendix interna; *Philarius imperialis* Kubo, Ras Abu Somer, male?; H, anterior carapace and rostrum, lateral; I, second pereiopod, carpus, dorsal; *Philarius gerlachei* (Nobili), Yenbo, female; J, third pereiopod (?), distal propod and dactyl.

Holthuis (1958). (c) *Harpiliopsis depressa* (Stimpson, 1860), 2 ovig. females, CLs 3.7, 4.4 mm, the larger with a rostral dentition of 6/4, the smaller with 6/5. Both specimens lack second pereiopods. The hepatic spine is situated at a much lower level than the antennal spine and so the specimens cannot belong to *H. beaupresii* (Audouin) and, as both specimens have a distinctly robust, stout body form, they are considered to belong to *H. depressa* rather than the slender *H. spinigera* (Ortmann), which has not yet been recorded from the Red Sea. *Harpiliopsis depressa* has been previously recorded from the Red Sea, first by Balss (1915). (d) *Coralliocaris superba* (Dana, 1852), 1 male, with a rostral dentition of 5/2. The specimen lacks both second pereiopods, but is identified as *C. superba* rather than *C. graminea* (Dana), both of which are known from the Red Sea, on account of the endopod of the third maxilliped having broadened segments.

Balss' material consists entirely of species now known to be associates of *Acropora* corals. *Periclimenes consobrinus* is an associate of pocilloporid corals, and examination of these hosts may reveal its presence in the Red Sea. *Periclimenes consobrinus* is known from Kenya, Tanganyika, Comoro Islands, La Réunion, Philippines, the Gulf of Thailand and the Great Barrier Reef.

Periclimenes pholeter Holthuis, 1973

Figs 22-23

Restricted synonymy

Periclimenes pholeter Holthuis, 1973: 30-35, figs 10-11.–Wear & Holthuis, 1977: 139.

Material examined. (i) 100 specimens (5 ovig. females), R.V *'Meteor'*, Cruise 5, stn 184, 19°27.6'N 38°43.3'S, 1825 m, traps, 26 Feb. 1987, coll. (ii) 1 male, 2 female, Naweni Point, Vanua Levu, Fiji, 16°48'15"S 179°34'30"E, anchialine pool near mangrove swamp, 19 July 1983, coll. S. Choy, RMNH, unnumbered.

Remarks. The Red Sea specimens agree, with one exception of one point noted below, with the description and figures provided of the type material.

In the original description the inferior orbital angle is illustrated as a slender, blunt, up-turned process, whereas in the present material this feature is represented by a broad subacute shelf-like projection. A specimen of *P. pholeter* from Aldabra, kindly provided by Prof. L.B. Holthuis, has the inferior orbital angle precisely as in the present specimens, and Dr C.H.J.M. Fransen has also confirmed that it is similar in the type material.

Also, in the type material, the rostral dentition varies from 1+9-10/2-4. In the present material eight specimens lack an epigastric tooth, so that the rostral dentition is 0-1+7-10/0-3, (82% with 1+9-10/1-2). The rostrum generally extends anteriorly to or beyond the end of the antennular peduncle. The dorsal carina is distinctly elevated and the ventral carina feebly developed. The proximal part of the ventral margin bears a vestigial double row of setae in some specimens, the distal portion being glabrous. A small tubercle is generally distinct, posterior to the epigastric tooth. The antennal spine is acute, marginal, slightly upwardly directed, distinctly larger than the hepatic spine. The corneal diameter appears similar in the present specimens and the type material, about 0.07 of the carapace length, with well-developed pigmentation and lacking a distinct accessory pigment spot. Out of 42 adult specimens sexed, only one proved to be male, which had the cornea of the right eye markedly reduced in size, that of the left appearing normal. The ophthalmic somite is without a bec ocellaire. The ventral medial margin of the proximal segment of the antennular peduncle bears a small acute tooth at about half its length. The scaphocerite is broadly rounded distally, feeble angled in the type specimen illustrated, with the lateral margin markedly thickened. The fourth thoracic sternite lacks a finger-like median process but bears a low transverse carina with a pair of blunt submedian teeth separated by a U-shaped notch. A similar carina is also present on the posterior fifth thoracic sternite. The third sternite is unarmed but the second bears a broad unarmed transverse ridge. The chelae of the second pereiopod are essentially as in the type specimens but in some specimens the palm is about 0.6 instead of 0.75 of the length of the chela and also possesses a pair of minute teeth proximally on the dactyls, with a single similar opposing tooth on the fixed finger. The dactyls of the ambulatory pereiopods are moderately compressed, with the unguis only feebly demarcated, about 0.4 of the corpus length, on the third pereiopod. The corpus is about 3.0 times longer than its proximal width, with a slender acute distal accessory tooth ventrally, less than half the length of the unguis. The distoventral spines of the propod are finely serrated along the dorsal margins. The dactyl of the fifth pereiopod is similar, but with a slightly reduced unguis. The distoventral propod is without distoventral spines but bears numerous serrulate spiniform cleaning setae. The endopod of the first pleopod, in the only male, shows a feeble indication of a small medial lobule, with the proximal half of the medial margin bearing seven plumose setae proximally and six small simple adpressed spinules distally; the distolateral margin hears 15 sparsely setulose setae. The appendix masculina of the male second pleopod is slightly longer than the appendix interna, with six long slender spines distally, some about 0.5 of the corpus length, with five ventrolateral distal spines and one ventromedial, some being minutely setulose. The telson is generally as in the type specimen but the submedian spines are less than the posterior marginal width of the telson, 1.75 times the submedian spine length. The submedian spines are finely setulose along the inner margin.

The minor details noted above leave no alternative to the conclusion that the Red Sea specimens from 1825 m are conspecific with the specimens from shallow

water. Even the corneal diameter does not appear to have undergone any significant reduction in size in the deep-sea specimens (0.7: ca. 0.08 of the carapace length) and is deeply pigmented. The original material, 16 specimens, was described from an anchialine fissure on the Sinai Peninsula, the Ras Muhammed Crack, and

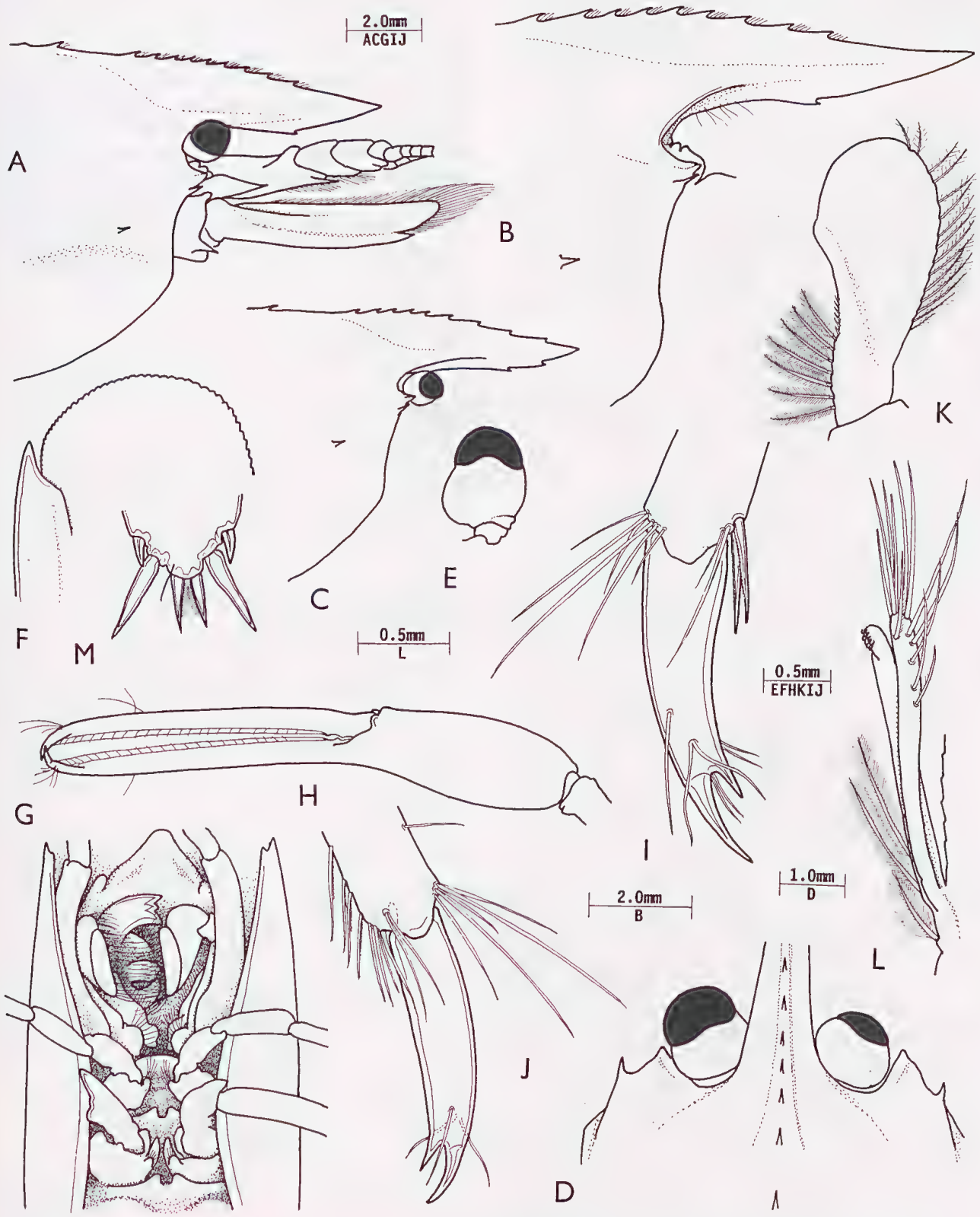

Fig.22. *Periclimenes pholeter* Holthuis, Red Sea. A, anterior carapace, rostrum, antennal peduncles; B,C, anterior carapace and rostrum; D, frontal region, dorsal; E, eye, dorsal; F, scaphocerite, distal end; G, anterior thoracic region; H, second pereiopod, chela; I, third pereiopod, dactyl and distal propod; J, fifth pereiopod, same; K, first pleopod, endopod; L, second pleopod, appendix masculina and appendix interna; M, posterior telson spines. A,B,E,F,G,H,I,J,M, female; C,D,K,L, male.

P. pholeter has also since been reported from anchialine pools on Aldabra, Seychelle Islands. The occupants of both the anchialine and deep-sea habitats are often held to be relict survivors from shallower waters. Hart, Manning & Iliffe (1985) mention several examples of crustacea occurring in shallow water marine caves, whose nearest relatives live at considerable depths. In no case reported does a single species occur in both zones. *Periclimenes pholeter* appears to be the first example of a decapod that has colonised and survived in both these habitats. The occurrence of *P. pholeter* at a depth of 1825 m may be partially explained by the hydrological conditions at this depth in the Red Sea. The water temperature at depths of 200 m or more is constant, between 21.5°C and 22°C (Türkay, 1986) and is therefore not as far removed from the anchialine habitat temperatures, 25.5°C (Holthius, 1973) as might otherwise have been expected. The presence of *P. pholeter* at 1825 m far exceeds the previously known maximal depth record for a palaemonid shrimp, held by *P. laccadivensis* (Alcock & Anderson) from 1285 m in the Laccadive Sea.

The occurrence of such large numbers in traps clearly indicates that substantial populations are involved. Few traps set in deep water have provided specimens of palaemonid shrimps and those that have been recorded have only been in small numbers of specimens (*Periclimenes* sp., King, 1984; Bruce, 1990a) (1 spm); *Periclimenes parvispinatus* Bruce, 1990b (1 spm); *Periclimenes poupini* Bruce, 1990a (6 spms). It is interesting to note that *P. pholeter* has biunguiculate ambulatory dactyls, usually an indication of involvement

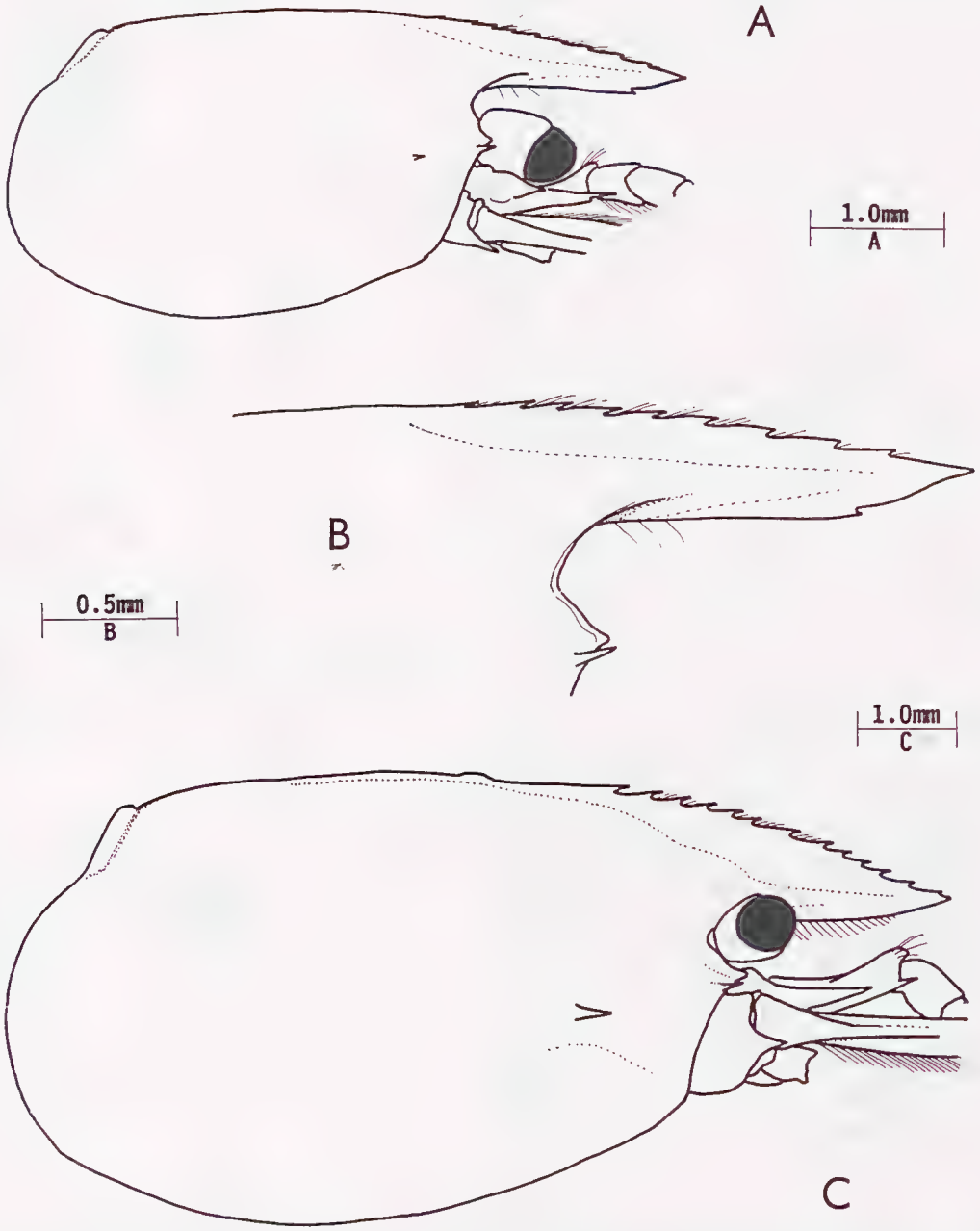

Fig.23. *Periclimenes pholeter* Holthuis, Red Sea, juvenile, CL 2.7 mm. A, carapace and antennular peduncles, lateral; B, rostrum. Fiji, ovigerous female, CL 7.8 mm; C, carapace and antennal peduncles.

in a commensal association in the Palaemonidae. All the other species from traps and most of the deep-sea pontoniine shrimps also have biunguiculate dactyls. *Periclimenes poupini* is known to be an associate of an anemone found on gastropod shells occupied by pagurids of the genus *Trizopagurus*. Even if the deep-sea specimens of *P. pholeter* have retained a commensal association with some host, it would appear that this habit has been lost or rendered unnecessary in the largely predator-free shallow water anchialine habitat, where there would be few suitable candidates for such an association. The marked preponderance of females in these deep-water specimens suggests that some form of hermaphroditism may occur in this habitat.

Several small juveniles are present in the collection. In the smallest specimens the rostrum is rather shallower than in the adults, about 0.58 of the carapace length, and not exceeding the antennular peduncle. The epigastric spine is lacking and the dorsal rostral carina bears about 9 low teeth, the proximal teeth particularly slender, with a single tooth ventrally. The cornea is about 0.15 of the carapace length, compared with about 0.08 in the adult.

Through the kindness of Dr C.H.J.M. Fransen, it has also been possible to examine three further specimens of *P. pholeter* from Fiji, (CLs 6.2, 6.6, 7.8 mm), collected by Dr S. Choy in an anchialine pool near mangrove habitats. These closely resemble the Red Sea - western Indian Ocean specimens, except that the rostrum is distinctly shorter, appearing deeper, and not exceeding the intermediate segment of the antennular peduncle. The rostral dentition is 12-13/10 and the smaller male and female specimens lack epigastric tooth. The rostral differences do not appear sufficient to suggest that these specimens should require separate specific status, although a subspecific designation might be appropriate. Until further material from the same region is available to indicate the full range of rostral variations, these specimens are considered to be conspecific with the previously known material. No other morphological differences could be detected between the two lots of specimens.

The ova of the single ovigerous female, CL 13.0 mm, are numerous and small, length about 0.5 mm.

Distribution. Type locality – Ras Muhammed Crack, Sinai Peninsula. Otherwise previously reported only from Aldabra, Seychelle Islands.

Periclimenes lanipes Kemp, 1922

Fig.24

Restricted synonymy

Periclimenes lanipes Kemp, 1922: 156-158, pl. fig.4.–Bruce, 1971a: 11-15; figs 3,4,5c,d.

Periclimenes (Harpilius) brooki.–Johnson, 1961: 59 (non *Anchistia Brockii* De Man, 1888).

Periclimenes brockii.–Johnson, 1979: 33 (non *Anchistia Brockii* De Man, 1898).

Material examined. 1 ovig. female, Singapore Straits, Fisheries Research Collection, stn 66, 50 m, 27 Jan. 1955, det. D.S. Johnson, (J.7879), ZRC 1989.89. (ii) male, Singapore Straits, Fisheries Research Collection, stn B60, 38-40 m, 14 Aug. 1955, det. D.S. Johnson (J.7878), ZRC 1989.2290.

Remarks. Johnson (1961, 1979) reported the occurrence of *P. brocki* in the Singapore Straits region. The material from the Zoological Reference Collection, National University of Singapore, has recently been re-examined and found it not to correspond to the species, *P. brocki*, reported as *Anchistia Brockii* from Ambon by De Man (1888). The female specimen is largely complete, with most appendages detached, and has a carapace length of 3.9 mm, with a rostral dentition of 11/1. It agrees precisely with the description provided by Kemp (1922), particularly with reference to the dense woolly setation of the pereiopods and is also at once distinguished from *P. brocki* (De Man) by the presence of an accessory tooth on the dactyls of the ambulatory pereiopods. The ambulatory dactyls are, as previously reported, densely provided with woolly setae, which largely obscure the dactyl. On cleaning and mounting a detached pereiopod it was also revealed that these setae also obscure several large spines on the distal propod, which were not reported by Kemp. Unfortunately, one spine was accidentally detached (indicated by dashed line) and its exact position could not be discerned with complete certainty. The merus is distoventrally acute, with four small mobile spines proximally, as reported by Kemp (1922), a feature not known in any other species of *Periclimenes*. The male specimen (CL 3.0 mm, R. 9/1) is similar, with all the pereiopods detached, except the minor second pereiopod, which is in an early stage of regeneration. The major chela has the palm about 1.4 times the carapace length. The first pleopod has the basipodite broad, about 1.6 times longer than wide, with the distolateral angle acutely produced, setose. The endopod is about 0.75 of the basipodite length, 3.0 times longer than wide, 0.6 of the endopod length. The medial margin bears a very small process at about 0.6 of its length, the proximal medial margin with 11 small simple spinules. The distal 0.6 of the lateral margin bears 13 short plumose setae and the distal margin is rounded, non-setose. The second pleopod has the basipodite 2.0 times longer than wide, about 1.25 times the first basipodite length, with the distolateral angle strongly produced, rounded, setose. The endopod is about 5.5 times longer than broad, subequal to the basipodite length, with the appendices at about 0.33 of the medial margin length. The appendix masculina has the corpus subcylindrical, about 0.3 of the endopod length, 7.0 times longer than wide, with three stout serrulate spines distally, the longest about 0.66 of the corpus length; the

distoventral margin bears three shorter, feebly spinulate spines. The appendix interna is slender, slightly shorter than the appendix masculina, with a few distal cincinnuli.

Periclimenes lanipes is an associate of gorgonocephalid basket-stars, but there is no record of any host for these Singapore specimens.

Distribution. Type locality – Mergui Archipelago, 12°48'N 98°16'10"E, 44 m. Also known from Somalia, Zanzibar, Madagascar, northern South China Sea, Queensland and New Caledonia.

Parapontonia nudirostris Bruce, 1968

Figs 25-27

Restricted synonymy

Parapontonia nudirostris Bruce, 1968: 1149-1156, figs 1-5.–Bruce, 1971: 18-19.–Bruce, 1981: 9,26.–Bruce, 1983: 204.

Material examined. (i) 1 male, 1 ovig. female, stn 34/0/1, Davies Reef, 18°50'S 147°39'E, 10 m, south reef front, 22 Oct. 1988, coll. K. Fabricius, NTM Cr.006837. (ii) 1 juv. male, 3 juveniles, stn 24/10/88, Davies Reef, 18°50'S

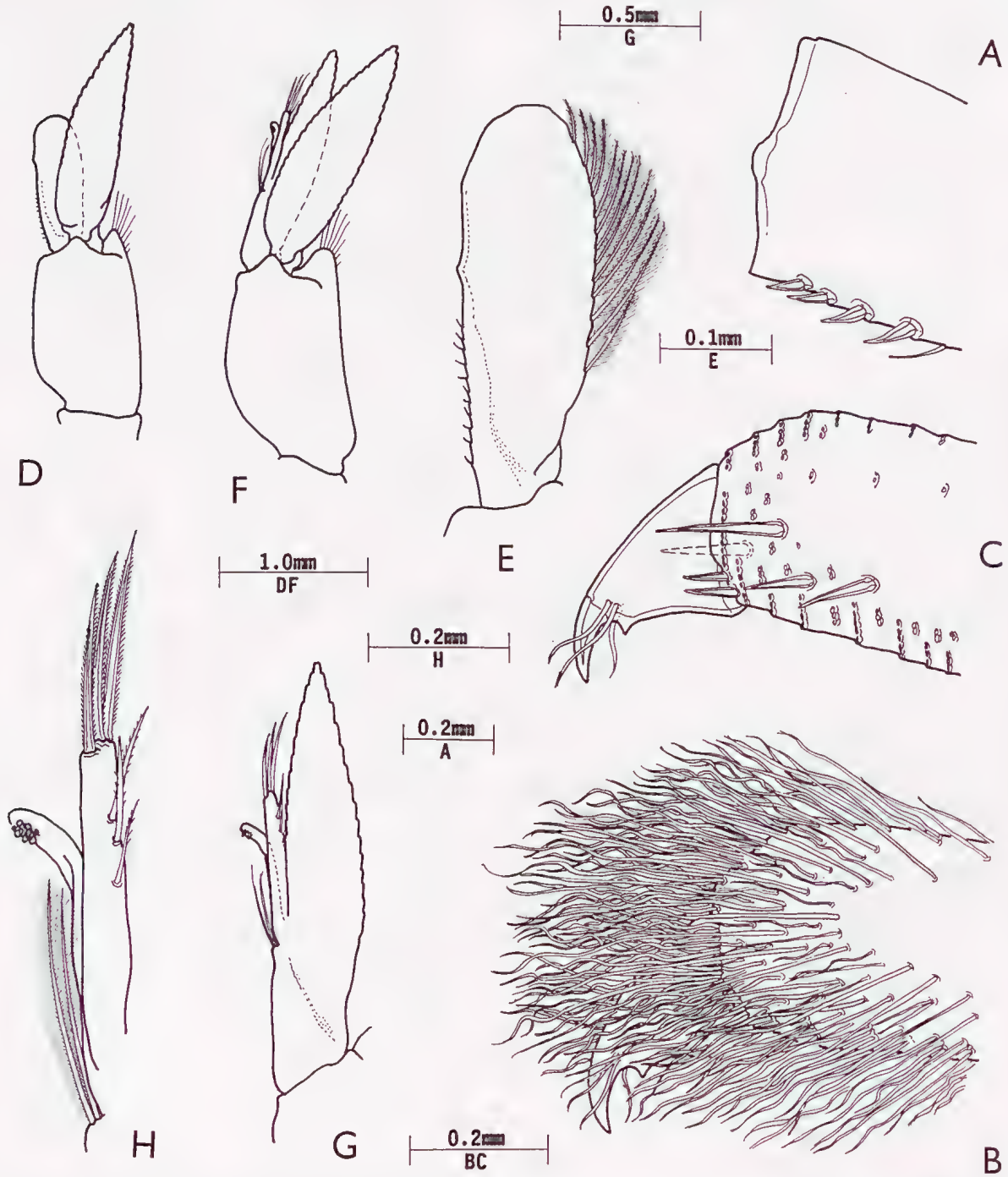

Fig.24. *Periclimenes lanipes* Kemp, Singapore Straits. A, third pereiopod (?), merus, distolateral angle; B, same, distal propod and dactyl; C, same, setae omitted; D, first pleopod; E, same, endopod; F, second pleopod; G, same, endopod; H, same, appendix masculina and appendix interna. A-C female; D-H, male.

147°39'E, 7 m, lagoon, 24 Oct. 1988, coll. K. Fabricius, NTM Cr. 006838.

Hosts. (i) *Tropiometra afra* (Hartlaub); (ii) *Himerometra robustipinna* (P.H. Carpenter) (Echinodermata, Crinoidea).

Remarks. The adult pair of specimens conform closely to the original description but some additional details can now be provided.

The cornea is conoidally produced but the process is not as conspicuously developed as in the type specimens. The second pereiopods of the male are more robust than in the holotype, with the major chela about 1.85 of the carapace length, about 2.8 times longer than the proximal depth, subcylindrical, slightly compressed and feebly swollen proximally. The fingers are robust, the dactylus about 0.5 of the palm length, instead of 0.9, with the dactyl 0.33 times longer than proximal depth, curved, with a stout curved tip, the cutting edge with four low blunt similar teeth over the central half of the cutting edge. The fixed finger is similar, with four similar low blunt teeth on the proximal half of the cutting edge length, with a further low tooth distally, separated from the fourth tooth by a deeper notch, with a deep notch adjacent to the stout tip into which the tip of the dactyl fits. The minor second pereiopod is similar, about 0.9 of the major pereiopod length. The dactyls of the ambulatory pereiopods are all distinctly biunguiculate, the propod robust, without distoventral or ventral spines. The endopod of the male first pleopod is about 0.45 of the exopod length, 4.0 times longer than central width, slightly curved medially, unexpanded, distally rounded and without a medial accessory lobule, the proximal half of the medial border with four very slender simple spiniform setae proximally and three shorter, stouter simple spinules distally, the distolateral margin bearing six stout feebly plumose setae. The endopod of the second pleopod bears the appendix masculina at about 0.5 of the length, the corpus is subcylindrical, feebly tapered distally with three ventromedial spines, densely serrulate, of increasing length distally, the longest spine terminal, about 1.25 times the corpus length, reaching to about 0.9 of the endopod length: the appendix interna is slender, distinctly exceeding the appendix masculina, with few distal cincinnuli only. The dorsal telson spines are very small, as in the type specimens, in the female at 0.54 and 0.77 of the telson length, the lateral posterior spines are distinctly larger than the dorsal spines, the intermediate spines are about 0.13 of the dorsal telson length, 6.5 times longer than the proximal width, robust and distally blunt, the submedian spines are about 0.5 of the intermediate spine length, very acute distally and setulose medially and laterally.

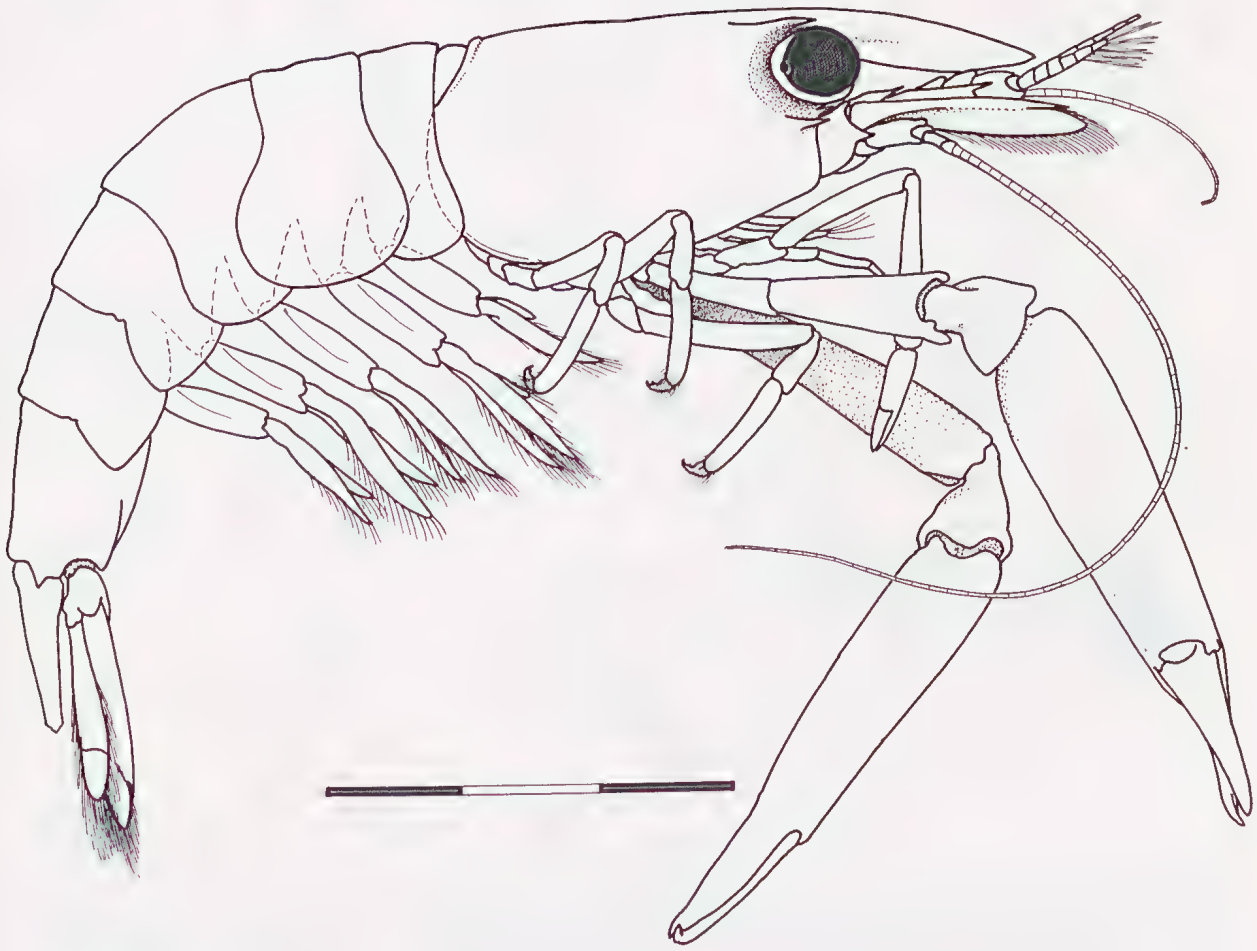

Fig.25. *Parapontonia nudirostris* Bruce, Davies Reef, male, scale bar in millimetres.

The juvenile specimens, particularly the smallest specimen, show a number of interesting features, which emphasise the close relationship of *Parapontonia* to the genus *Periclimenes*, and illustrate their disappearance with growth. In the smallest specimen, CL. 1.1 mm, the orbit is already of the adult form, deep, with a well-

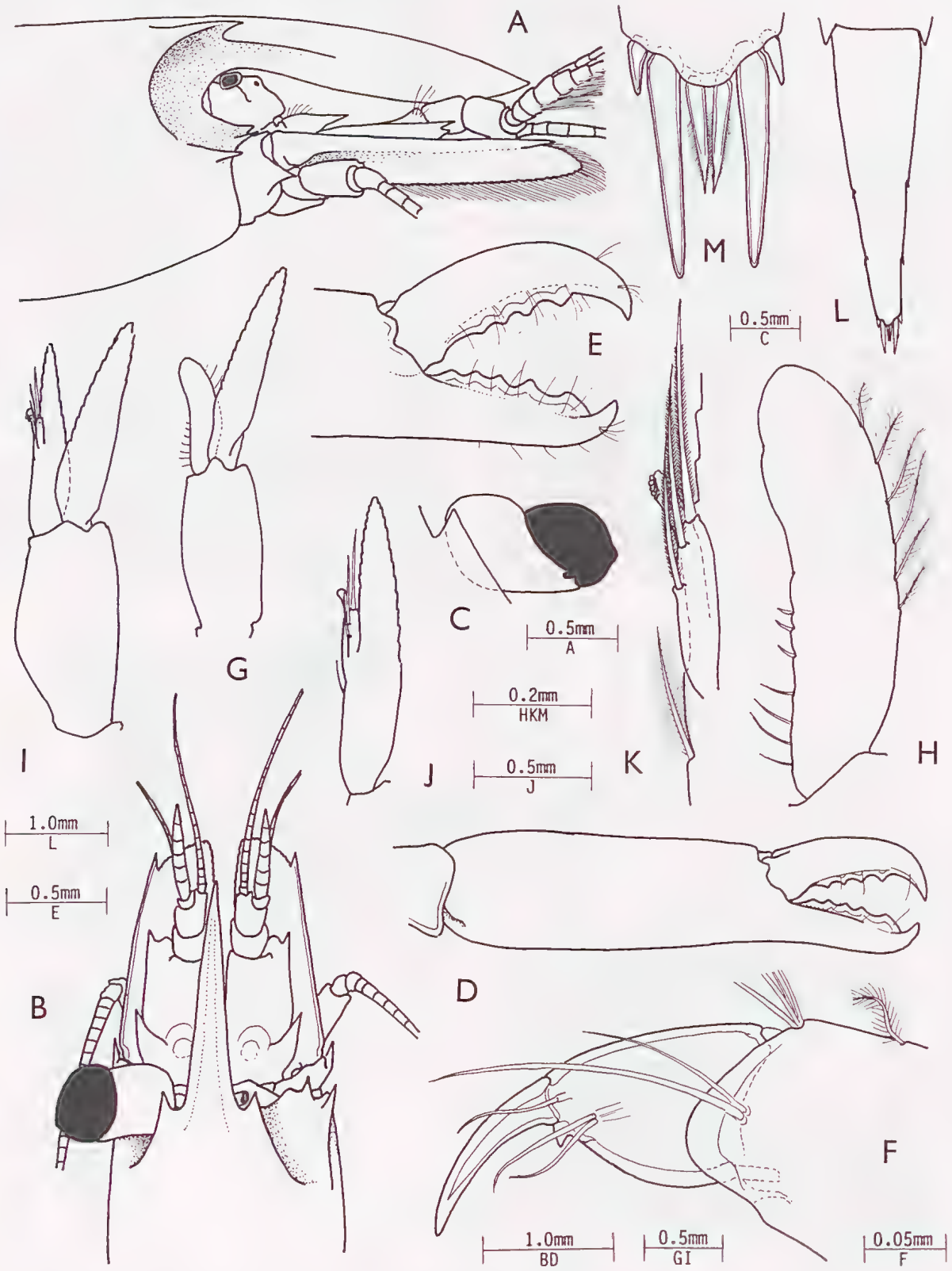

Fig.26. *Parapontonia nudirostris* Bruce, Davies Reef, male. A, anterior carapace, rostrum and antennal peduncles, lateral; B, same, dorsal; C, eye; D, major second pereiopod, chela; E, same, fingers; F, third pereiopod, distal propod and dactyl; G, first pleopod; H, same, endopod; I, second pleopod; J, same endopod; K, same, appendix masculina and appendix interna; L, telson; M, same, posterior spines.

Fig.27. *Parapontonia nudirostris* Bruce, Davies Reef, juveniles. A, anterior carapace and appendages, dorsal; B, carapace and rostrum, lateral; C, antennule; D, second pereiopod, chela; E, same, fingers; F, third pereiopod, propod and dactyl; G, same, distal propod and dactyl; H, carapace and rostrum, lateral; I, eye; J, second pereiopod, chela; K, same fingers; L, third pereiopod, distal propod and dactyl; M,N, second pereiopod chela, fingers; O, first pleopod, endopod; P, second pleopod, endopod. A-G, CL 1.1 mm; H-L, CL 1.6 mm; M, CL 1.7 mm; N-P, CL 1.8 mm.

developed supraorbital tooth and the antennal and hepatic spines in their adult positions. The rostrum is about 0.75 of the carapace length, but with three small acute distal teeth. The cornea is globular, without any trace of a distal conoidal process. It seems most likely that the juveniles of those species of *Periclimenes* in which the cornea is conoidally produced, once placed in a separate subgenus *Corniger* Borradaile, 1915, will also have globular or hemispherical corneae in their juvenile stages and subsequently be liable to misidentification. The second pereiopods are about 0.95 of the carapace length, the fingers 0.68 of the palm length, with a single small acute tooth on the cutting edge of the fixed finger, the cutting edge of the dactyl entire. The ambulatory propods are robust, about 4.4 times longer than the central width, and with a single minute distoventral spine. The dactyl is very similar to that of the adult, with a distinct acute ventral accessory tooth. The antennule has the rami of the upper flagellum fused for the two proximal segments, with shorter free ramus of one segment, with four groups of aesthetascs, and the longer free ramus of 7 segments. The lower flagellum has 7 slender segments. The stylocerite is well developed and the statocyst contains a small ovoid statolith. The next largest specimen, with a carapace length of 1.6 mm, has lost the rostral teeth and also the spinule on the distoventral angle of the ambulatory propod. The accessory tooth on the ambulatory dactylus is rather poorly developed. The cornea remains globular and the fixed finger of the second pereiopod chela has three small acute teeth, with a single similar tooth on the dactylus. The next larger specimen, carapace length 1.7 mm, shows further development of the second pereiopod chela, with three small acute teeth on the dactylar cutting edge and the further incipient development of a fourth distal tooth on the fixed finger. The largest specimen, CL. 1.8 mm, still with a globular cornea, is a juvenile male with the second pereiopod bearing a fusiform appendix masculina with a single finely serrulate distal spine, about 1.4 times the length of the corpus; the appendix interna far exceeds the corpus of the appendix masculina. The endopod of the first pleopod is about 4.0 times longer than wide, with four feeble simple spinules proximomedially and four short plumose setae distolaterally. The chela of the second pereiopod is more robust, with three dactylar teeth and four on the fixed finger.

The adults of the genus *Parapontonia* are distinguished from those of *Periclimenes* by the lack of rostral teeth, presence of well-developed epistomal horns and conoidal corneal processes, all features that may be present in some *Periclimenes* species (see *P. amboinensis* above). These characters are not present in the early juvenile stages, which appear to be indistinguishable from *Periclimenes*. The only species of *Periclimenes* so far described that lacks rostral teeth is *P. insolitus* Bruce, an echinoid associate known only from Hawaii, which has hemispherical corneae and lacks epistomal horns.

Parapontonia nudirostris has been previously reported in association with both the present hosts.

Distribution. Type locality – Tiaré Bay, Nouméa, New Caledonia. Also previously reported from several Queensland localities, North Stradbroke Island, Heron Island, One Tree Island, Lizard Island and Sudbury Reef.

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Hyperiid Amphipods (Crustacea: Amphipoda: Hyperiidea) Collected Recently from Eastern Australian Waters

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ABSTRACT. A taxonomic report on hyperiid amphipods collected during the period 1970-1977 from waters off New South Wales, and in 1989 from off Sydney and slightly north-east of Brisbane, is presented. The collection consists of sixty one species of which nineteen are new records for Australian waters. Taxonomic features of all of the latter, and some of the lesser known species, are illustrated. A brief diagnosis and a list of synonymies is given for each species and remarks on systematics to aid future identification and comments on taxonomic difficulties are provided where appropriate. Most of the species represent a tropical or warm-temperate fauna indicating the influence of warm-core eddies in the Tasman Sea.

ZEIDLER, W., 1992. Hyperiid amphipods (Crustacea: Amphipoda: Hyperiidea) collected recently from eastern Australian waters. Records of the Australian Museum 44(1): 85–133.

The hyperiid amphipod fauna of Australian waters has not received much attention in the past. Previous records of hyperiids, mainly from eastern Australia, are by Barnard (1931), Dakin & Colefax (1940), Stebbing (1888), Young & Anderson (1987), and Zeidler (1978). Watson & Chaloupka (1982) record a few species from Bass Strait. Very few of these papers provide a taxonomic treatment of the species studied and our knowledge of the Australian fauna is thus limited with identifications relying on the availability of a variety of, often difficult to obtain, literature concerning fauna from other parts of the world.

Previous to this study, seventy four species of hyperiids were known from Australian waters (Young & Anderson, 1987; Zeidler, 1978); nearly all records being from the shallower (less than 400 m) waters of eastern Australia. In most cases hyperiids were only collected as part of a general sampling program and it is thus likely that many more species will be added to the Australian fauna in the future. In particular there are very few plankton samples available from deep water (greater than 1000 m) which is the domain of most Physosomata which represent about one third of the world's fauna of about 240 species. Also opening and closing nets were rarely used so that information on the depth preference of species in Australian waters (and indeed worldwide) is very limited.

Since 1971, the New South Wales State Fisheries (now the Fisheries Division of the NSW Department of Agriculture) has been carrying out trawling surveys

along the coast of New South Wales, sometimes extending north to Queensland or south to Bass Strait using their research vessel the *Kapala*. On a few occasions plankton samples were collected resulting in a small but interesting collection of hyperiid amphipods.

The present paper is a report on the collections made between 1971 and 1977 (Appendix I) although most of the species have come from the 1971 and 1972 trawls when an Isaacs-Kidd midwater trawl was used. Also included in this study is a small collection made in 1989 from off Sydney by HMAS *Cook* and from slightly north-east of Brisbane by the CSIRO research vessel *Franklin* (Appendix I). The collection is significant for its faunal richness comprising 61 species of which 19 are new records for Australian waters including four belonging to the Lanceolidae, a family that has not previously been recorded from Australia. Most of the species are typical of a tropical or warm-temperate fauna and this is probably due to the influence of the warm-core eddies which frequent the eastern coast of Australia (Young & Anderson, 1987). The presence of some rare species such as *Vibilia caeca* Bulycheva, 1955 which has only been recorded in the literature on one other occasion (Vinogradov, 1956) and *Oxycephalus longipes* Spandl, 1927 which has not been recorded since the original description, together with the recognition of several species previously 'lost' in synonymy, indicates how little the Hyperiidea have been studied worldwide. This paper therefore adds significantly to the knowledge of the Australian fauna and the systematics of hyperiids in general.

Most species of hyperiids have a worldwide distribution, occurring in water masses having similar physicochemical properties. Thus, many species found in the northern hemisphere also occur in Australian waters and it is not unreasonable to expect that representatives of most of the world's fauna of hyperiids will eventually be found in Australian waters. With this in mind researchers should initially refer to Bowman & Gruner (1973) for diagnoses and keys to families and genera before proceeding with the local literature. Vinogradov *et al.* (1982) provide, apart from general information, keys to families, genera and most currently recognised species together with useful illustrations, but the text is in Russian and the publication is probably not readily available to most researchers. A key to Australian species is not given here but will be provided in a forthcoming publication on hyperiids from south-eastern Australia, which will also include many new records, some new species and an updated checklist of hyperiids from Australian waters. However, a brief diagnosis is given for each species to facilitate identifications, particularly of those not illustrated. A list of synonymies for each species is also provided but I have not given a full list of references or misidentifications as these would have added unnecessarily to the text.

The material on which this paper is based is deposited in the collections of the Australian Museum (AM); representative examples of some species have been deposited in the South Australian Museum (SAM). The systematic arrangement follows that of Bowman & Gruner (1973) with genera and species arranged alphabetically except for Brachyscelidae which I have recognised as a separate family closely related to *Eupronoe* (Pronoidae). Specimen length was measured along a lateral parabolic line drawn from the anterior extremity of the head through the middle of the body to the posterior limit of the telson. All species which are new records for Australian waters have been illustrated. The following abbreviations are used in the illustrations: A1, A2 = first and second antenna; G1, G2 = first and second gnathopod (or pereopod); P3-7 = third to seventh pereopod; Mxp = maxilliped; U1-3 = first to third uropod; Us = urosome including uropods and telson, and f and m are used to indicate female or male specimens.

Systematic Section

Suborder Hyperiidea

Infraorder Physosomata

Scinidae

Scina Prestandrea, 1833

Remarks. Species of *Scina* are generally found in deeper waters (greater than 200 m) (Vinogradov *et al.*, 1982) and since few plankton collections in deep water have been made in Australian waters there are few Australian records of this genus. Of the thirty six species currently recognised (Zeidler, 1990), only three have previously been recorded from Australia. Species of *Scina* can be difficult to distinguish but Wagler (1926) and Vinogradov *et al.* (1982) provide good illustrations and a revised key to the world species is given by Zeidler (1990).

Scina crassicornis (Fabricius)

Astacus crassicornis Fabricius, 1775: 415.
Hyperia cornigera Milne-Edwards, 1830: 387.
Clydonia gracilis Dana, 1853: 834, pl.55 fig.6a,b.
Tyro atlantica Bovallius, 1885: 14.
Tyro sarsii Bovallius, 1885: 15.
Scina edwardsi Garbowski, 1896: 103, pl.1 fig.2, pl.3 figs 19-33, pls 4-7, pl.8 figs 97-109.
Scina crassicornis var. *bermudensis* Shoemaker, 1945: 228, fig.31.

Material examined. 78 females (7.0 - 13.2 mm), 28 males (3.4-13.4 mm) from stations JP 71-2 (AM P39746 - 2 f, 4 m); JP 71-3 (AM P39747 - 50 f, 13 m; SAM C4205 - 10 f, 5 m); JP 71-4 (AM P39748 - 2 f); JP 71-7 (AM P39749 - 7 f, 3 m); JP 71-8 (AM P39750 - 6 f, 3 m) and JP 77-25 (AM P39751 - 1 f).

Diagnosis. Antenna 1 as long as body. Outer lobes of maxilliped about 3 times as long as wide, tapering for distal half to acute, rounded, point. Pereopods 1-7 with normal articles. Pereopod 5 a little longer than pereopod 6. Pereopod 7 slightly longer than half pereopod 6. Pereopod 5, article 2, both margins finely serrate, subequal in length to articles 3-7 combined, anterodistal projection reaching to first quarter of article 4; article 4, length subequal to article 5; article 6, length about one quarter article 5; dactyl a very small nail. Pereopod 6, dactyl long about half article 6, sometimes curved upwards. Pereopod 7, dactyl much shorter than that of pereopod 6 but longer than that of pereopod 5. Uropods 1 and 2, inner margins with fine serrations; exopods extremely short, spine-like.

Remarks. Many of the specimens in this collection had the long dactyl of pereopod 6 curved upwards, a feature I also found common among specimens from the western North Pacific Ocean (Zeidler, 1990) but not mentioned in the literature previously. Variation in the relative lengths of articles 4 to 6 of pereopod 6, similar to *S. curvidactyla* Chevreux, 1914, were also common. Similar variations in the relative length of segments of pereopods 5 to 7 have been noted by previous authors but are not considered to be of taxonomic significance (Hurley, 1956; Thurston, 1976; Brusca, 1978). Although *S. crassicornis* is most similar to *S. curvidactyla* it is easily distinguished from this and other species of *Scina* by the relatively short, feeble article 6 of pereopod 5 and by the relatively longer dactyl of pereopod 6. In most other *Scina* species the dactyls of pereopods 5 to 7 are of similar length.

Eleven ovigerous females ranging in size from 9.2 to 12.8 mm were captured in March (JP 71-3, 71-8).

Distribution. *Scina crassicornis* is a cosmopolitan species occurring approximately between the polar circles (Brusca, 1978). It was first recorded from Australian waters by Young & Anderson (1987).

Scina lamperti Vosseler

Fig.1

Scina lamperti Vosseler, 1901: 110-113, pl.9 figs 1-7.
Scina uncipes lamperti.–Wagler, 1926: 348-350, figs 13b,14.

Material examined. 2 females (4.4 and 6.2 mm) from station JP 71-7 (AM P39752).

Diagnosis. Antenna 1 about one third as long as body. Outer lobes of maxilliped two and one half times as long as wide, pointed terminally. Pereopods 3 and 4, article 6, posterodistal corner incised distally, approaching subchelate ending. Pereopod 6, length about two thirds pereopod 5 but a little longer than pereopod 7. Pereopod 5, article 2, both margins slightly serrate, distinctly longer than articles 3-7 combined, anterodistal projection extending slightly beyond article 3; article 4, length subequal to article 5; article 6, length about half article 5. Pereopods 5 and 6, dactyl a short nail. Pereopod 7, articles relatively thick with articles 4-6 wider than half length; dactyl blunt-ended with distinctive gland (?) duct. Uropods 1 and 2, inner margins with fine serrations (very fine for uropod 2); exopods very short, spine-like.

Remarks. *Scina lamperti* has not been recognised in recent times and has been considered a subspecies of *S. uncipes* Stebbing, 1895 (Wagler, 1926) or a synonym of *S. spinosa* Vosseler, 1901 together with *S. uncipes* and *S. spinosa affinis* Wagler, 1926 (Vinogradov *et al.*, 1982). Wagler (1926) recognised four subspecies amongst what he called "die *uncipes* - Gruppe": *S. uncipes uncipes*, *S. uncipes lamperti*, *S. spinosa spinosa* and *S. spinosa affinis*. The former two are similar in that the inner lobe of the maxilliped is only about one fourth as long as the outer lobes, pereopod 7 has very thick articles and the dactyl is blunt-ended with what appears to be a gland duct. The latter two are also similar but differ from the former two in that the inner lobe of the maxilliped is about half as long as the outer lobes, pereopod 7 has relatively thinner articles and the dactyl is a small curved nail without a gland (?) duct. Wagler's description of *S. u. lamperti* (a male) differs from Vosseler's (1901) original description in that the outer lobes of the maxilliped are less pointed and the second article of pereopod 5 is slightly shorter than articles 3 to 7 combined. The two specimens at hand however, agree in detail with Vosseler's description and are distinguished from other species of *Scina* by the following combination of characters: i) the inner lobe of the maxilliped is one fourth as long as the outer lobes; ii) the outer lobes of the maxilliped are pointed; iii) the sixth article of pereopods 3 and 4 are incised distally, approaching a subchelate ending; iv) the second article of pereopod 5 has only slightly serrated margins and is distinctly longer than articles 3 to 7 combined; v) the articles of pereopod 7 are relatively thick with articles 4 to 6 wider than half the length; vi) the dactyl of pereopod 7 is blunt-ended with a distinctive gland (?) duct. I believe that these characters combined with other minor features are sufficient to warrant the resurrection of *S. lamperti* as a valid species. *Scina uncipes*, although similar to *S. lamperti*, is readily distinguished by article 6 of pereopods 3 and 4 which is not incised distally (at most the posterior margin is slightly projected above the insertion of setae) and by article 2 of pereopod 5 which has strongly serrated margins and is distinctly shorter than articles 3 to 7 combined.

Scina uncipes most closely resembles *S. spinosa* and Stebbing (1904: 23), in a discussion of the genus, states, "*Scina spinosa*, Vosseler, 1901 found on a female specimen 3-5 mm long, 'perhaps not quite full-grown', should not, I think, be separated from *S. uncipes*, which I founded in 1895 on a male specimen 7.5 mm long". However, I regard the differences in the maxilliped and pereopod 7, already mentioned, as significant at the

specific level and for the moment, both species should be regarded as valid. As for *S. spinosa affinis*, this variety or subspecies, is just like *S. spinosa* as described by Vosseler (1901), except that the serrations on article 2 of pereopod 5 and on the inner margin of uropod 1 are less numerous and not as strong. I doubt that these features alone are of specific significance and that *S. s. affinis* can be distinguished from the normal variation found in *S. spinosa*. Shoemaker (1945), who had specimens with characters overlapping both *S. s. spinosa* and *S. s. affinis*, confirms this view.

Distribution. Vosseler (1901) recorded *S. lamperti* from the equatorial North Atlantic and Wagler (1926) from the Indian Ocean near the Seychelles. Other records are lost due to past synonymies with *S. uncipes*

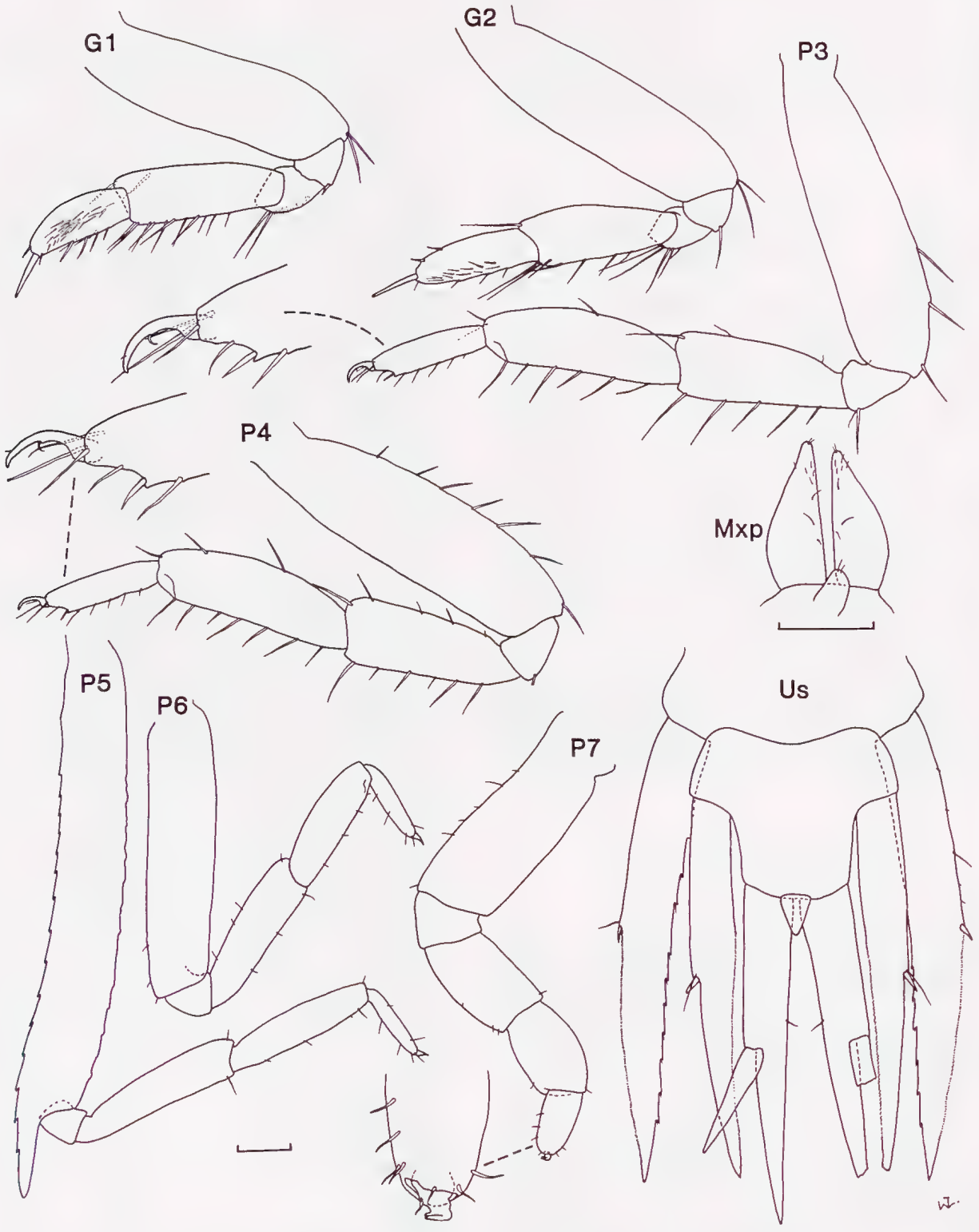

Fig.1. *Scina lamperti* Vosseler, female 6.2 mm (scales = 0.2 mm).

or *S. spinosa*. This is a new record for Australian waters.

LANCEOLIDAE

Lanceola Say, 1818

Remarks. Like the previous genus, species of *Lanceola* are usually found in deep water (1000-8000 m), but none have previously been recorded from Australian waters. Vinogradov *et al.* (1982) recognise twelve species and provide the only satisfactory key (in Russian), together with useful illustrations.

Lanceola loveni Bovallius

Fig.2

Lanceola loveni Bovallius, 1885: 6-7.
Lanceola aestiva Stebbing, 1888: 1309-1313 (part).

Material examined. 1 male (damaged, approximately 8 mm) from station JP 71-8 (AM P39753).

Diagnosis. Pereonite 7 and all pleonal segments with feeble, dorsal denticles. Pereopods 3-7 with very slender articles. Pereopod 4 subequal in length to pereopod 5 or slightly shorter; both about three quarters as long as pereopod 6. Pereopod 7, length slightly less than half pereopod 6. Pereopod 6 distinctly longer than pereon. Telson, length about half peduncle of uropod 3.

Remarks. The present specimen differs slightly from Bovallius' (1885) description in that pereopods 5 and 7 are relatively shorter in relation to pereopod 6. However, it is in total agreement with the figures given for this species by Shoemaker (1945). Characteristic features are the short telson and the relatively slender pereopods 3 to 6 with pereopod 6 being considerably longer than pereopod 4. *Lanceola loveni* is most similar to *L. serrata*, Bovallius, 1885, but in *L. serrata*, article 5 of gnathopod 1 is more expanded distally with a small anterior lobe partly overlapping article 6 and the

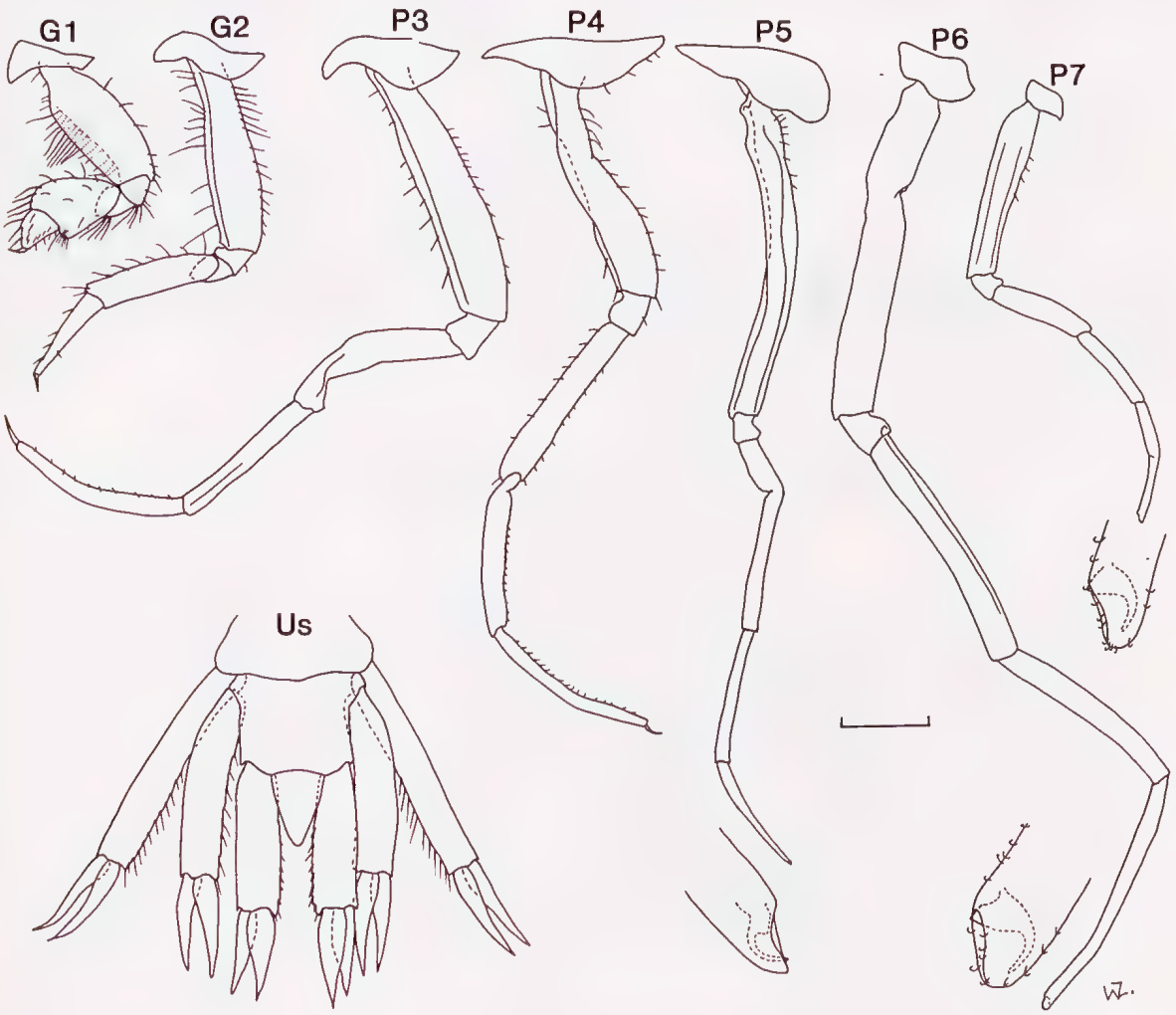

Fig.2. *Lanceola loveni* Bovallius, male approximately 8.0 mm (scale = 1.0 mm).

telson is much longer than half of the peduncle of uropod 3.

This species is usually found in depths greater than 1000 m (Vinogradov, 1957) and the present record from about 600 m is one of the shallowest reported (Thurston, 1976).

Distribution. North Atlantic and north-west Pacific but past confusion of this species with *L. aestiva*, Stebbing, 1888 (Thurston, 1973), may mean that it has a much wider recorded distribution. This is a new record for Australian waters.

Lanceola pacifica Stebbing

Fig.3

Lanceola pacifica Stebbing, 1888: 1302-1306, pls 151, 152. *Lanceola pacifica* var. *robusta* Woltereck, 1909: 160.

Material examined. 5 females (damaged, approximately 18-27 mm) from stations JP 77-26 (AM P39754; 3 f) and JP 77-28 (AM P39755; 2 f) and 1 male (?) (7.5 mm) from station JP 71-7 (AM P39756).

Diagnosis. Pereon and pleon without dorsal denticles. Pereopod 4 slightly shorter than pereopod 5. Pereopod 5, length about two thirds pereopod 6. Pereopod 7, length about half pereopod 6. Pereopod 6 distinctly longer than pereon. Telson slightly longer than peduncle of uropod 3.

Remarks. Although the female specimens are damaged the material can readily be identified as *L. pacifica* and differs from Stebbing's (1888) description only in that the telson is more pointed. The immature male (?) also appears to be this species but the telson is just shorter than the peduncle of uropod 3. *Lanceola pacifica* is very similar to *L. sayana* Bovallius, 1885, but in *L. sayana* the head has a well-developed, although short, rostrum, especially in females, which is absent in *L. pacifica*.

Juveniles tend to occur in shallower depths (0-300 m) than adults (2000-4000 m) (Thurston, 1973) which is in line with the present findings.

Distribution. Widely distributed in tropical and

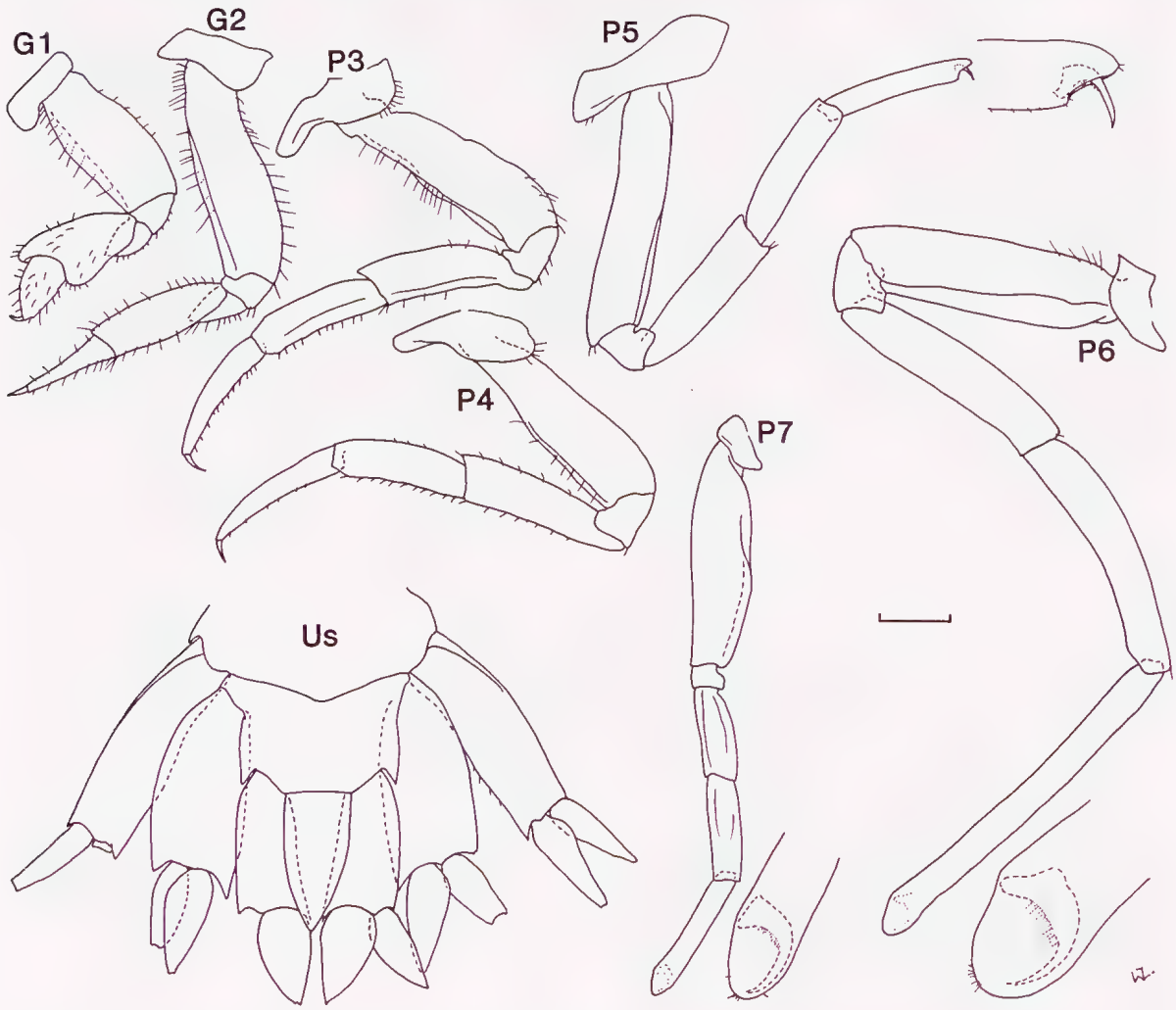

Fig.3. *Lanceola pacifica* Stebbing, female 27.0 mm from station JP 77-28 (scale = 1.0 mm).

temperate regions. This is a new record for Australian waters.

Lanceola sayana Bovallius

Fig.4

?*Lanceola pelagica* Say, 1818: 318.
Lanceola sayana Bovallius, 1885: 7, fig.1,1a,1b.
Lanceola sayana var. *longipes* Woltereck, 1909: 158-159, pl.6 figs 16,18b.
Lanceola sayana var. *typica* Woltereck, 1909: 158-159, pl.6 figs 17,18a.
Lanceola pelagica.–Shoemaker, 1945: 206, fig.14.

Material examined. 2 females (21.5 and 23.0 mm) from stations JP 77-19 (AM P39757) and JP 77-27 (SAM C4206).

Diagnosis. Pereon and pleon without dorsal denticles. Head with small hooked rostrum, more prominent in females. First antennae, distal articles fused. Pereopod 4 slightly shorter than pereopod 5. Pereopod 5, length about two thirds pereopod 6. Pereopod 7, length about half pereopod 6. Pereopod 6 distinctly longer than pereon. Telson slightly longer than peduncle of uropod 3.

Remarks. Unlike other species of *Lanceola*, *L. sayana* is frequently found in relatively shallow depths but is most common from 1000 to 2000 m extending to 3000 m (Vinogradov *et al.*, 1982). Apart from *L. pacifica*, *L. sayana* is also similar to *L. felina* Bovallius, 1885 and *L. intermedia* Vinogradov, 1960, but is most readily distinguished from these two species by antenna 1 in which the distal articles are fused and by the relative length of pereopod 6 which is much longer than the pereon.

Distribution. A widely distributed species including the Antarctic Ocean. It is a new record for Australian waters.

Megalanceola Pirlot, 1935

Remarks. Species of this genus are some of the largest hyperiids known with a total length of about 100 mm. They are usually found in deeper water (about 1000 m), but have not previously been recorded from Australian waters. *Megalanceola* is similar to *Lanceola* but is easily distinguished by the anteriorly bent nature of specimens and the relatively larger eyes. Only two species of *Megalanceola* are currently recognised (Vinogradov *et al.*, 1982). *Megalanceola remipes* (Barnard, 1932) can easily be distinguished from *M. stephenseni* (Chevreux, 1920), illustrated here, by pereopods 3 to 5 which have very wide articles, particularly articles 4 to 6.

Megalanceola stephenseni (Chevreux)

Fig.5

Lanceola sp. Stebbing, 1888: 1308, fig.27.
Lanceola stephenseni Chevreux, 1920: 4-7, figs 1-3.
Megalanceola terrae-novae Pirlot, 1935: 2, figs 1-4.

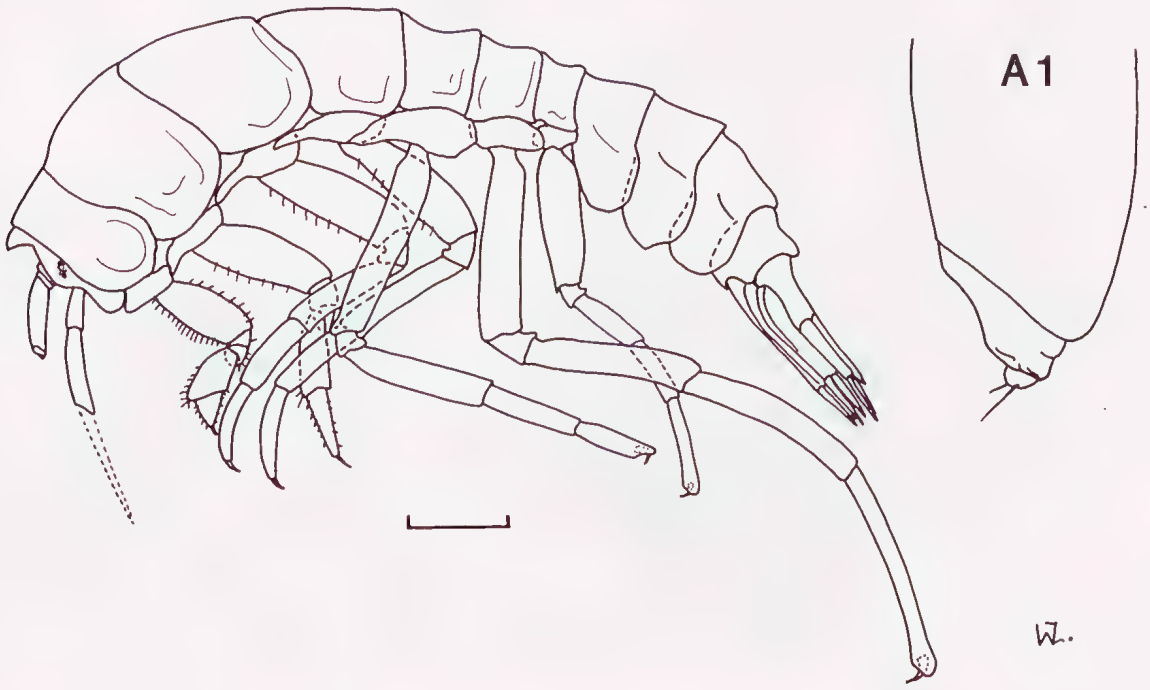

Fig.4. *Lanceola sayana* Bovallius, female 21.5 mm from station JP 77-19 (scale = 2.0 mm).

Material examined. 2 females (60 and 64 mm) from stations JP 77-26 (AM P39758) and F25 (AM P40876).

Diagnosis. Mandibular palp, article 2 distinctly longer than article 3. Gnathopods 1 and 2, articles 2-6 very setose. Pereopods 3-7 with slender articles. Pereopods 3 and 4, dactyl normal, not retractable.

Remarks. The present specimen agrees with the description and figures given by Chevreux (1920) and Pirlot (1939). It seems to be a rare species, judging by records in the literature.

Distribution. *Megalancoela stephenseni* has been recorded from near the Azores (Chevreux, 1920), near Newfoundland (Pirlot, 1935), near Bermuda (Shoemaker, 1945), from the "Southern Ocean" (Herring, 1981), and probably from the Banda Sea (Stebbing, 1888) according to Shoemaker. This is a new record for Australian waters.

Infraorder PHYSOCEPHALATA

VIBILIIDAE

Vibilia Milne-Edwards, 1830

Remarks. Species of *Vibilia* are very similar in gross morphology and, apart from a few distinctive species, most require expert knowledge for a correct identification and a revision of the genus is long overdue. Vinogradov *et al.* (1982) recognise 17 species and provide a useful key (in Russian).

Vibilia armata Bovallius

Vibilia armata Bovallius, 1887: 10.
Vibilia gracilis Bovallius, 1887: 9.
Vibilia gracilenta Bovallius, 1887: 9-10.
Vibilia erratica Chevreux, 1892: 32, figs 1-3.

Material examined. 2 males (8.4 and 8.8 mm) from station JP 71-3 (AM P39759).

Diagnosis. Pereon and pleon broad, robust. Pleonites with median ventral points. Antenna 1 shorter than head and first 2 pereonites; flagellum elongated, lanceolate, almost diamond shaped, ending in sharp point terminally. Gnathopod 2, anterior border of article 6 slightly produced; carpal process about as long as article 6. Pereopods 3-6, dactyls strong, length about half article 6. Pereopod 7, article 2 rectangular, slightly dilated posteriorly, two thirds as wide as long, length equivalent to articles 3-5. Lateral corners of last urosomite produced, partly overlapping peduncle of uropod 3. Uropod 3, peduncle distinctly longer than rami. Telson, triangular, pointed terminally.

Remarks. The combination of characters given in the diagnosis, particularly the shape of antenna 1 and the urosome, readily distinguish *V. armata* from all its congeners.

Distribution. Widely distributed in tropical and temperate regions. Previous records from Australian waters are by Barnard (1931), Guiler (1952), Watson & Chaloupka (1982), Young & Anderson (1987) and Zeidler (1978).

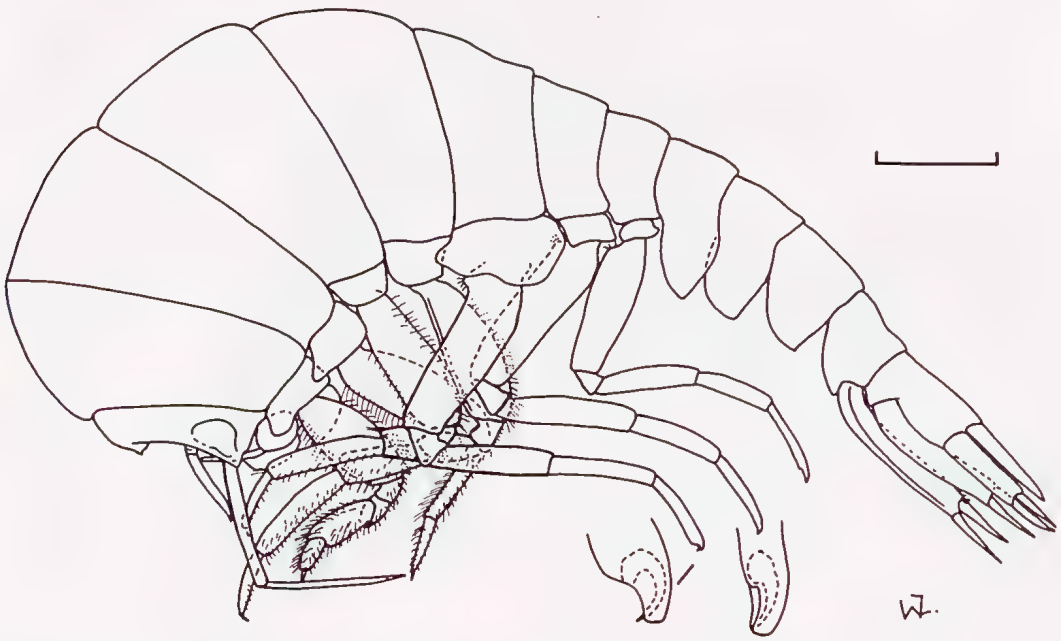

Fig.5. *Megalanceola stephenseni* (Chevreux), female 52.0 mm (scale = 5.0 mm).

Vibilia caeca Bulycheva

Fig.6

Vibilia caeca Bulycheva, 1955: 1050.

Material examined. 1 female (6.1 mm) from station JP 71-8 (AM P39760).

Diagnosis. Eyes absent. Pleon distinctly broader than pereon. Antenna 1 inserted midlaterally on head, as long as head and pereonites 1-3; flagellum elongate, lanceolate, excised on ventral margin for distal half. Gnathopod 2, carpal process almost as long as article 6. Pereopods 3-6, dactyls as long, or almost as long, as half article 6. Pereopod 7, article 2 rectangular, almost twice as long as wide with small, sharp, anterodistal projection and rounded posterodistal lobe overlapping article 3, length equivalent to articles 3-5. Lateral corners of last

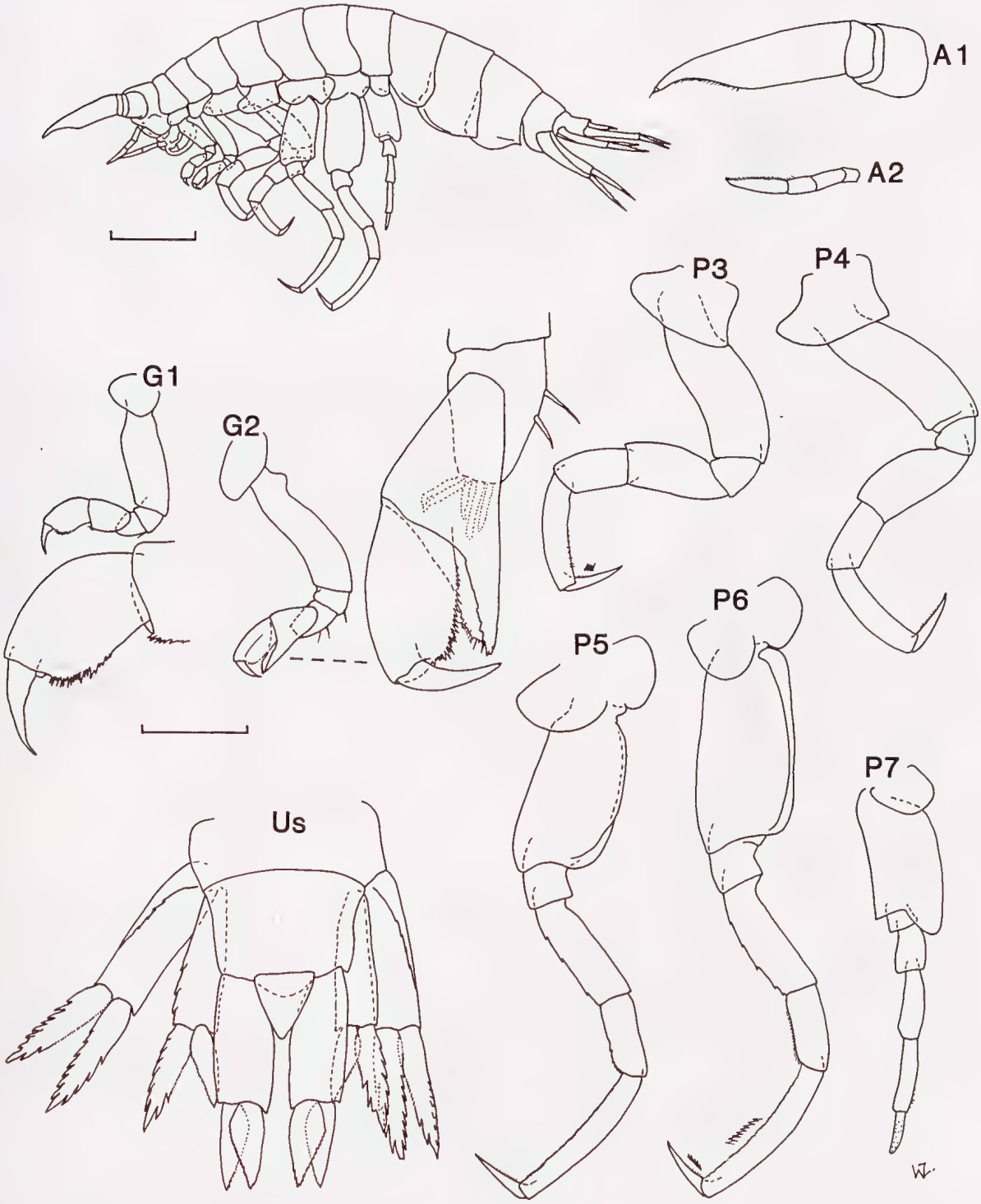

Fig.6. *Vibilia caeca* Bulycheva, female 6.1 mm (scales = 1.0 mm, 0.5 mm).

urosomite not produced. Uropod 3, peduncle distinctly longer than rami. Telson, triangular, pointed terminally.

Remarks. The present specimen agrees in detail with the description given for this species by Bulycheva (1955) and with the description and figures given by Vinogradov *et al.* (1982). *Vibilia caeca* most closely resembles *V. australis* Stebbing, 1888, but the absence of eyes is a unique feature amongst species of *Vibilia*.

Distribution. Previously it has only been recorded from the north-west Pacific Ocean (Bulycheva, 1955) and the western Bering Sea near the Kuril Islands (Vinogradov, 1956). It is a new record for the southern hemisphere and Australian waters.

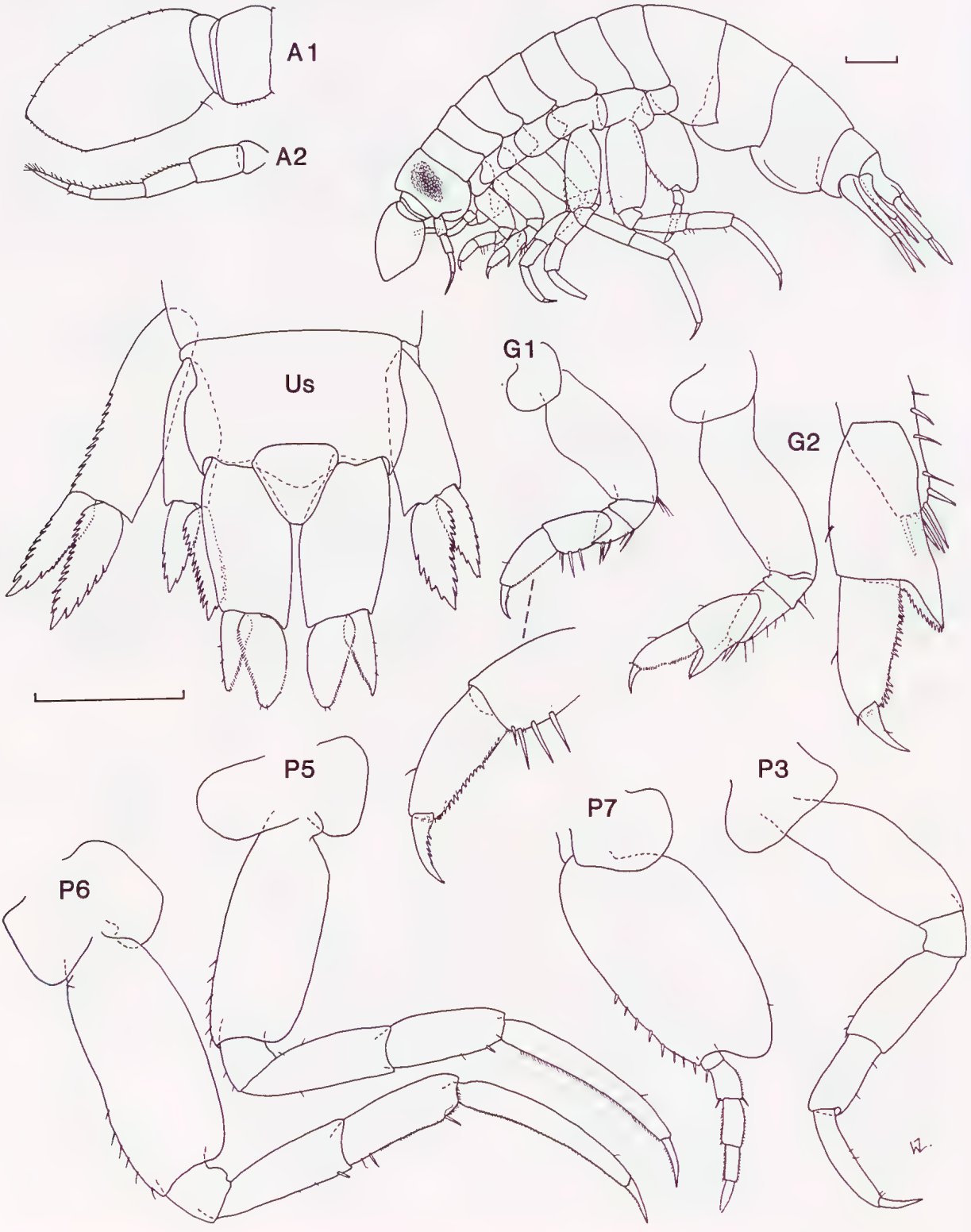

Fig.7. *Vibilia chuni* Behning & Woltereck, male 5.8 mm (scales = 0.5 mm).

Vibilia chuni Behning & Woltereck

Fig.7

Vibilia chuni Behning & Woltereck, 1912: 8-9, figs 7,8.
Vibilia hodgsoni Stewart, 1913: 251-253, pl.6 figs 1-6.

Material examined. 1 male (5.8 mm) from station JP 71-2 (AM P39761).

Diagnosis. Pereon and pleon broad. Antenna 1 shorter than head and first 2 pereonites; flagellum oval-shaped, ventral margin oblique for distal third. Gnathopod 2, carpal process about half length article 6. Pereopods 3-6, dactyls much shorter than half article 6, about one quarter article 6 for pereopods 5 and 6. Pereopod 7, article 2 rectangular, almost twice as long as wide, half as long again as articles 3-7 combined, with rounded margins and rounded posterodistal lobe overlapping article 3. Lateral corners of last urosomite produced, partly overlapping peduncle of uropod 3. Uropod 3, peduncle distinctly longer than rami. Telson, triangular, rounded terminally.

Remarks. A relatively rare species. Males have a second antenna with 6 or 7 articles as is usual in *Vibilia* but are further distinguished from females by the slightly larger eyes and by the inner ramus of uropod 3 which is broader and apically rounded.

The combination of characters given in the diagnosis, particularly the shape of antenna 1, the urosome and pereopod 7, readily distinguish *V. chuni* from all its congeners.

Distribution. Known from widely separated records in tropical and temperate regions. It is a new record for Australian waters although Tranter (1977) recorded it from the north-eastern part of the Indian Ocean off Western Australia.

Vibilia cultripes Vosseler

Fig.8

Vibilia cultripes Vosseler, 1901: 121-123, pl.11 figs 6-18.

Material examined. 1 male (11.4 mm) from station JP 71-3 (AM P39762).

Diagnosis. Pereon and pleon broad. Antenna 1, length equivalent to head and first pereonite; flagellum oval-shaped, distal margin rounded. Gnathopod 2, carpal process about two thirds length article 6. Pereopods 3-6, dactyls shorter than one quarter article 6. Pereopod 7, article 2 rectangular, about two thirds as wide as long, slightly longer than articles 3-5 with slight posterodistal lobe barely overlapping article 3; articles 5 and 6 with distinct, rounded anterodistal process; article 7 pointed with knife-like anterior margin. Lateral corners of last urosomite produced, partly overlapping peduncle of uropod 3. Uropod 3, peduncle about as long as inner ramus. Telson, rounded, almost circular.

Remarks. An uncommon species. It most closely resembles *V. longicarpus* Behning, 1913, but distinctive features are the form of gnathopod 2 and of pereopod 7 and the absence of a terminal tooth on the inner ramus of uropod 3 which is replaced by two, usually widely separated, teeth; particularly evident in males.

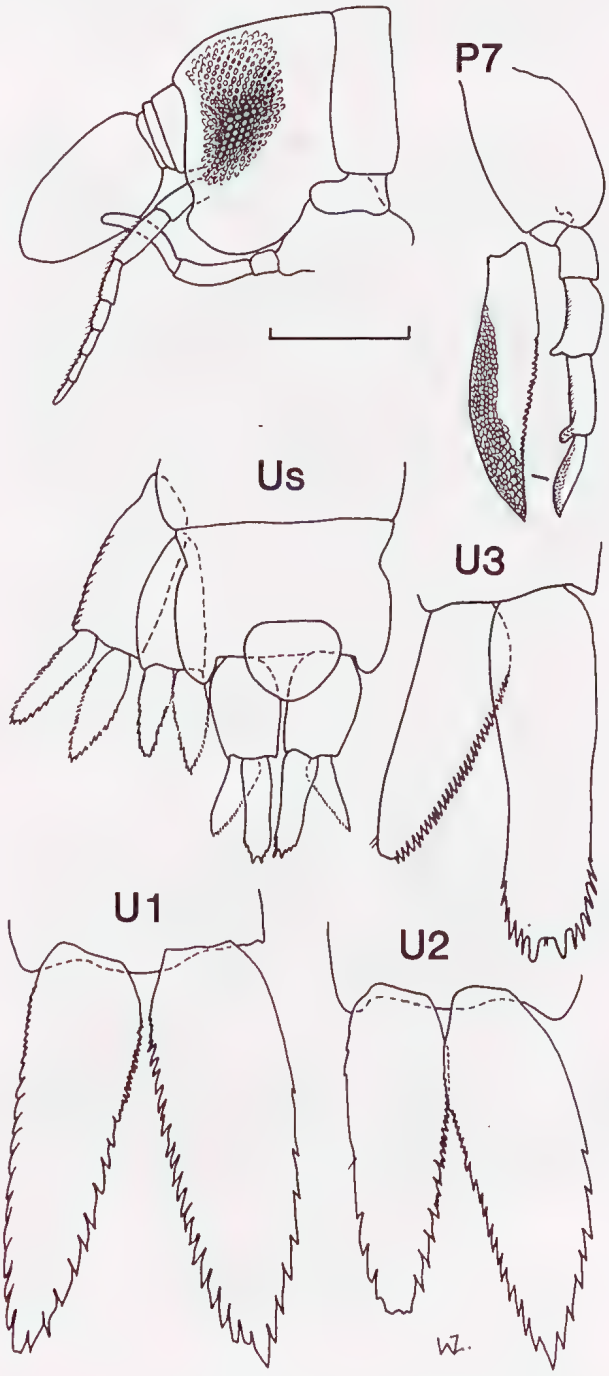

Fig.8. *Vibilia cultripes* Vosseler, male 11.4 mm. U1-3 from left (scale = 1.0 mm).

Distribution. Widely distributed in tropical and temperate regions, particularly the Atlantic. It was first recorded from Australian waters by Young & Anderson (1987).

Vibilia stebbingi Behning & Woltereck

Vibilia stebbingi Behning & Woltereck, 1912: 5-6, figs 1-3.

Material examined. 73 females (5.5-11.8 mm) and 35 males (5.0-9.8 mm) from stations JP 71-2 (AM P39763 - 36 f, 15 m; SAM C4207 - 10 f, 5 m); JP 71-3 (AM P39764 - 11 f, 7 m); JP 71-4 (AM P39765 - 2 f); JP 71-7 (AM P39766 - 9 f, 5 m); JP 71-8 (AM P39767 - 4 f, 2 m) and JP 72-23 (AM P39768 - 1 f, 1 m).

Diagnosis. Body distinctly broader in middle. Antenna 1 slightly shorter than head and first 3 pereonites; flagellum, dorsal and ventral margins parallel, distal margin oblique. Gnathopod 2, carpal process about half length article 6. Pereopods 3 and 4, dactyls about half length article 6. Pereopods 5 and 6, dactyls about one third length article 6. Pereopod 7, article 2 rectangular, almost twice as long as wide, slightly longer than articles 3-5 with small, sharp anterodistal projection and rounded posterodistal lobe overlapping article 3. Lateral corners of last urosomite not produced. Uropod 3, peduncle distinctly longer than rami. Telson, triangular, pointed terminally.

Remarks. *Vibilia stebbingi* seems to be closely related to *V. viatrix* Bovallius, 1887 and, in the shape of antenna 2 and the urosome, also resembles *V. antarctica* Stebbing, 1888. However, in both of these species the process of article 5 of gnathopod 2 is as long as article 6 and article 2 of pereopod 7 is of a slightly different shape, without a pointed, anterodistal process.

This was the most common species of *Vibilia* in the present collections. Young & Anderson (1987) also found this species to be very common in warm-core eddy J (Cresswell, 1983) off eastern Australia.

Two ovigerous females (6.6 and 10.2 mm) were captured in March (JP 71-8, 71-4).

Distribution. Widely distributed in tropical and temperate regions; particularly abundant when salp swarms occur (Dick, 1970). Despite its relative abundance in eastern Australian waters the first Australian record was by Young & Anderson (1987).

CYSTISOMATIDAE

Cystisoma Guérin-Méneville, 1842

Remarks. Specimens of *Cystisoma*, although large, are very fragile and rarely collected. In the past there was a tendency to describe new species almost every time another specimen was encountered and the genus is in need of revision. Vinogradov *et al.* (1982) recognise five species and provide the only useful key (in Russian).

Cystisoma pellucida (Willemöes-Suhm)

Fig.9

?*Cystisoma neptunus* Guérin-Méneville, 1842: 215, pl.1 fig.1.
Thaumatops pellucida Willemöes-Suhm, 1874: 634, pl.49 fig.1.
Cystisoma spinosum spec. B.–Stebbing, 1888: 1325-1329, pl.155.
Thaumatops longipes spec. B.–Bovallius, 1889: 47-52, pl.3 figs 2-4, 14.
Thaumatops parkinsoni.–Stephensen, 1918: 66-68, fig.29 (only in reference to *T. longipes* spec. B of Bovallius, 1889).

Material examined. 1 damaged male (?) (approximately 80 mm) from station JP 77-22 (AM P39769).

Diagnosis. Antenna 1 of female as long as head, expanded, diamond-shaped terminally. Mandible with 1 central spine, lateral spines absent. Oral spines, 4-6 pairs arranged in arched rows anteriorly to buccal mass. Pereopod 7 prehensile with small, curved dactyl, length of dactyl less than half maximum width article 6. Urosome (including uropods) distinctly longer than pleon. Uropods, exopodites about twice as long as endopodites with parallel sides and pointed, triangular terminal margin.

Remarks. *Cystisoma pellucida* is readily distinguished from all its congeners by the unusual form and length of the uropodal exopods; in all other species the exopods are lanceolate and rarely much longer than the endopods. The prehensile nature of pereopod 7 with its small dactyl is also a distinctive feature of this species.

Distribution. Known from widely separated records in tropical and temperate regions. It is a new record for Australian waters.

PARAPHRONIMIDAE

Paraphronima Claus, 1879

Remarks. This is the only genus in this distinctive family and currently consists of two species (Brusca, 1981). Although very similar in appearance, both species are readily separated by the characters given in the following remarks on *P. gracilis*

Claus, 1879.

Paraphronima crassipes Claus

Paraphronima crassipes Claus, 1879a: 7-8, pl.1 figs 6-9, pl.2 fig.10.
Paraphronima clypeata Bovallius, 1885: 11, fig.2.
Paraphronima pectinata Bovallius, 1887: 13-14.
Paraphronima cuivis Stebbing, 1888: 1337-1342, pl.157.

Material examined. 3 females (11.2, 11.6 and 16.6 mm), 2 males (7.5 and 9.8 mm) from stations JP 71-2 (AM P39770 - 1 m); JP 71-3 (AM P39771 - 1 f; SAM C4208 - 1 f) and JP 71-7 (AM P39772 - 1 f, 1 m).

Diagnosis. Head slightly longer than deep. Pereonites 1-4 approximately equal in width. Pleonite 1 with anterior margin nearly perpendicular to body. Pereopods 5-7, anterior margin of articles 3-6 with few or no spines (even under high magnification). Pereopod 7 only slightly shorter than pereopod 6.

Remarks. One ovigerous female (11.6 mm) was captured in March (71-7).

Distribution. Widely distributed in tropical and temperate regions. Previous records from Australian waters are by Barnard (1931), Guiler (1952), Sheard (1965) and Young & Anderson (1987).

Paraphronima gracilis Claus

Fig.10

Paraphronima gracilis Claus, 1879a: 7-8, pl.1 figs 4,5.
Paraphronima edwardsi Bovallius, 1885: 12.

Material examined. 1 male (4.0 mm) from station F 33 (AM P39503).

Diagnosis. Head slightly shorter than deep. Pereonites 1-2 much narrower than pereonite 3. Pleonite 1, anterior margin forms acute angle with body axis. Pereopods 5-7, anterior margin of articles 3-6 with several, small spines. Pereopod 7 only as long as articles 1-5 of pereopod 6.

Remarks. This species closely resembles the previous one and Hurley (1956) even suggested (but rejected) the idea that *P. crassipes* may be a later moult stage of *P. gracilis*; the former species tends to be larger and more robust than the latter. However, *P. gracilis* is readily distinguished by the presence of numerous spines on the anterior margins of pereopods 5 to 7, by the distinctly shorter pereopod 7 compared to pereopod 6, and by the shape of the pleonites, particularly pleonite 1 the anterior margin of which forms an acute angle with the body axis (almost perpendicular in *P. crassipes*). According to Brusca (1981), the spination of pereopods 5 to 7 and the shape of pleonite 1 are particularly reliable characters.

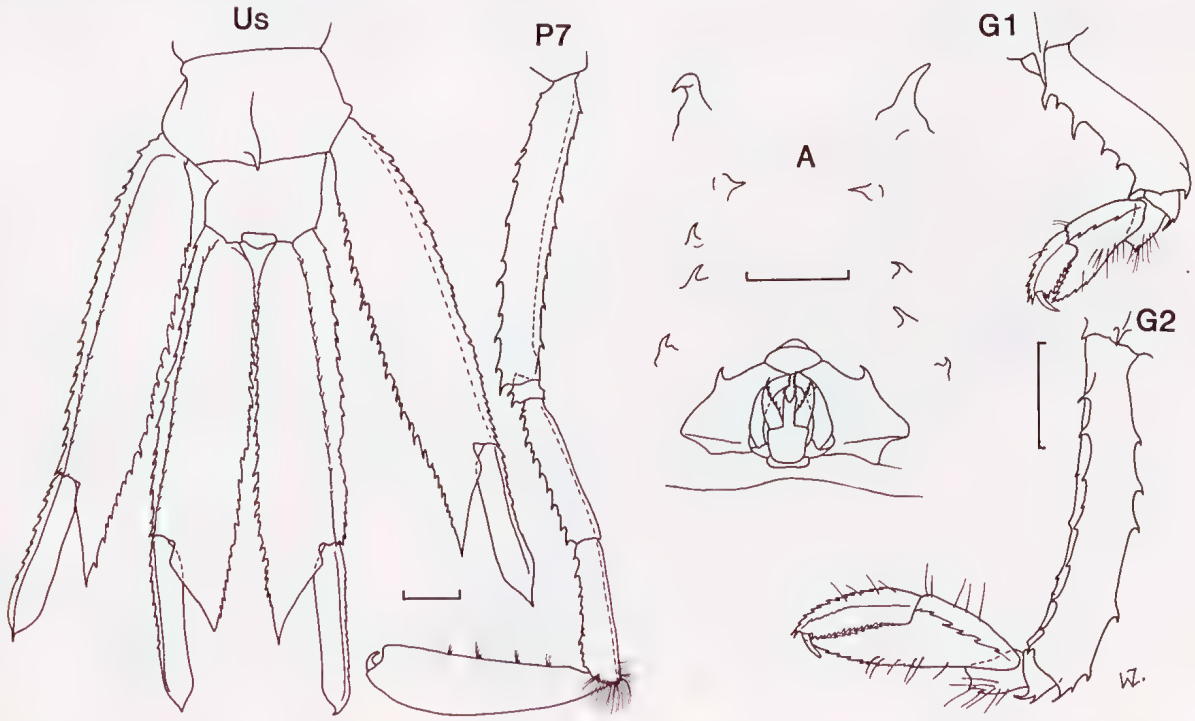

Fig.9. *Cystisoma pellucida* (Willemöes-Suhm), male approximately 80.0 mm. A, ventral part of head around buccal mass (scales = 2.0 mm).

Distribution. Widely distributed in tropical and temperate regions. It is a new record for Australian waters although Tranter (1977) recorded it from the north-eastern part of the Indian Ocean off Western Australia.

HYPERIIDAE

Hyperia Latreille, *in* Desmarest, 1823

Remarks. This genus has been revised by Bowman (1973) who provides a key and very useful illustrations for each species. Bowman recognised eight species, one of which, *H. antarctica* Spandl, 1927, is now regarded a synonym of *H. spinigera* Bovallius, 1889 (Thurston, 1977). More recently two additional species of *Hyperia* have been described; *H. bowmani* Vinogradov, 1976 and *H. curticephala* Vinogradov & Semenova, 1985.

Hyperia spinigera Bovallius

Fig.11

Hyperia spinigera Bovallius, 1889: 191-194, pl.10 figs 33-39.
Hyperia antarctica Spandl, 1927: 153-156, fig.2.

Material examined. 1 female (7.8 mm) from station JP 71-4 (AM P39773).

Diagnosis. Pleonite 1, posterior corner rounded. Pleonites 2-3 with small points midventrally. Pleonite 3 sometimes with strongly convex posterior margin. Antenna 1 of female digitiform, not slender as is usual in *Hyperia*. Mandibular palp articles subequal. Gnathopods 1 and 2, articles 2-4 with long setae on posterior parts of distal margins; article 6 with setae (sometimes long) on both margins. Gnathopod 1, posterodistal corner of article 5 rounded, not produced into carpal process, with setae of varying lengths, sometimes nearly as long as article 6. Gnathopod 2, carpal process short with long setae. Pereopods 3 and 4, article 2 with cluster of setae on posterodistal corner; articles 4-6, posterior margin with dense covering of short spinules (in typical *H. spinigera*). Pereopods 5-7 unarmed except for cluster of setae on anterodistal corner of article 2. Telson slightly longer than width at base, length slightly more than half peduncle, uropod 3.

Remarks. The present specimen most closely resembles *H. antarctica* Spandl, 1927 as described and figured by Bowman (1973), particularly in the form of uropod 3 and in that articles 5 and 6 of pereopods 3 and 4 are completely unarmed, even when viewed with high magnification. Thurston (1977) however, has shown that *H. antarctica* is merely a developmental form of *H. spinigera*. In addition to the above features, the present specimen also differs from typical *H. spinigera* in that the spines on the gnathopods are fewer in number and generally the ornamentation resembles that of *H. crassa* Bowman, 1973.

Distribution. Widely distributed in both northern and southern hemispheres. It is a new record for Australian waters although it has been recorded from New Zealand (Hurley, 1955) and Antarctic waters (Spandl, 1927; Hurley, 1960).

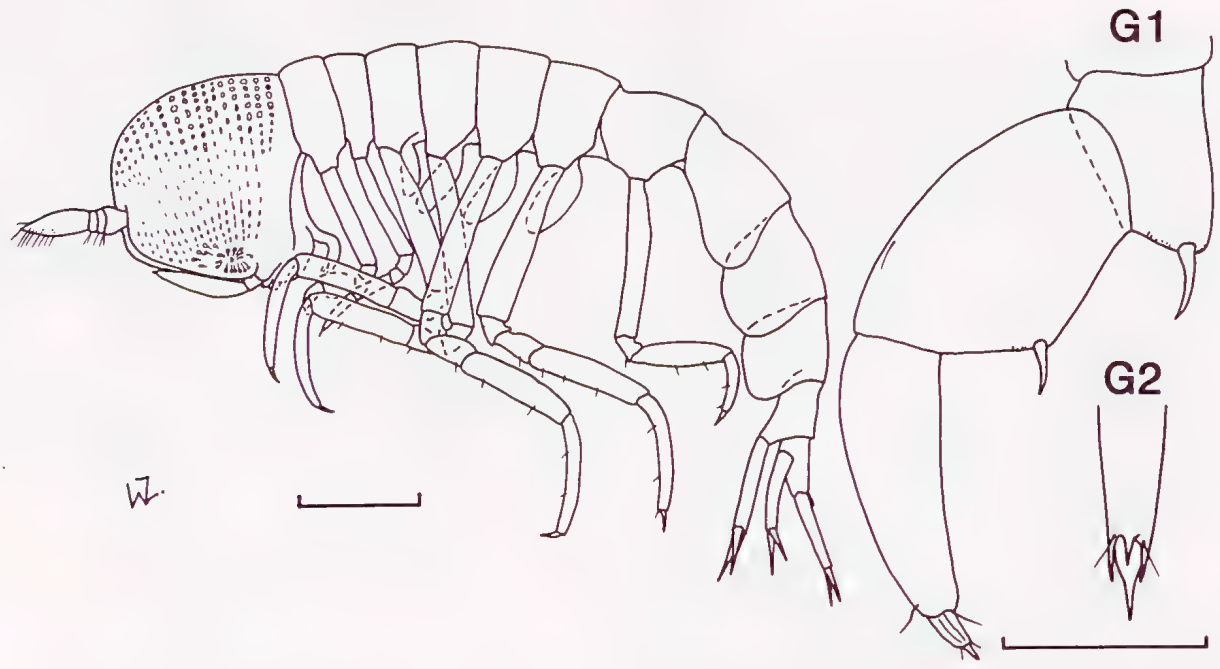

Fig.10. *Paraphronima gracilis* Claus, male 3.8 mm (scales = 0.5 mm, 0.1 mm).

Hyperioides Chevreux, 1900

Remarks. There are currently only two species in this distinctive genus of Hyperiidae, both are represented in the present collection. It has been revised by Bowman (1973), who provides illustrations for each species.

Hyperioides longipes Chevreux

Hyperioides longipes Chevreux, 1900: 143-145, pl.17 fig.2. *Hyperia sibaginis* var. *longipes*.–Vosseler, 1901: 63.

Material examined. 1 male (3.5 mm) from station F 33 (AM P39502).

Diagnosis. Head nearly straight dorsally. Eye facets limited to dorsal part of head. Antenna 1 of female with 2 articles, length almost twice antenna 2. Gnathopod 2, carpal process reaching middle of article 6. Uropod 3, peduncle about twice as long as wide, slightly longer than exopod.

Remarks. This species is readily distinguished from its congener by the eye facets which are limited to the dorsal part of the head.

Distribution. It has been recorded from warm parts of all the world's oceans. First recorded from Australian waters by Bowman & McGuinness (1982) who found it to be relatively abundant off Western Australia, although Tranter (1977) recorded it from the north-eastern part of the Indian Ocean.

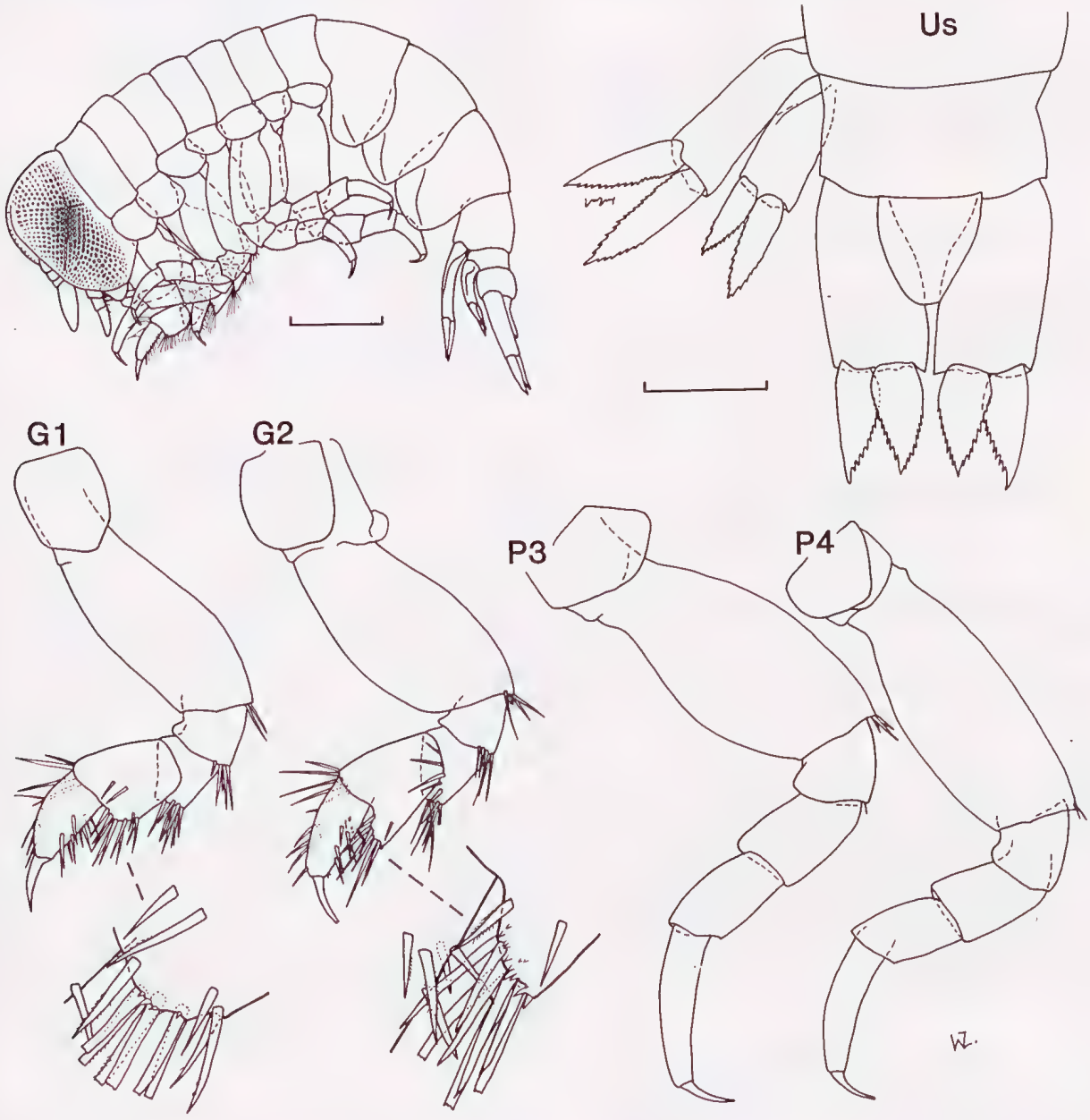

Fig.11. *Hyperia spinigera* Bovallius, female 7.8 mm (scales = 1.0 mm, 0.5 mm).

Hyperioides sibaginis (Stebbing)

Hyperia sibaginis Stebbing, 1888: 1379-1382, pl.165.

Material examined. 8 females (1.2-2.7 mm) and 14 males (2.4-3.9 mm) from stations JP 89-2 (AM P39774 - 4 f, 1 m) and JP 89-3 (AM P39775 - 4 f, 13 m).

Diagnosis. Head rounded dorsally. Eye facets cover dorsal and lateral parts of head. Antenna 1 of female with 3 articles, length slightly longer than antenna 2. Gnathopod 2, carpal process small, reaching to one quarter article 6. Uropod 3, peduncle length at least two and one half times width; exopod length about two thirds peduncle.

Remarks. One ovigerous female (2.7 mm) was captured in April (JP 89-2).

Distribution. Widely distributed and relatively common in tropical and temperate regions. Previous records from Australian waters are by Barnard (1931), Bowman & McGuinness (1982) and Zeidler (1978).

Hyperoche Bovallius, 1887

Remarks. Species of this genus are distinguished by the distinctly chelate gnathopods. Vinogradov *et al.* (1982) recognise seven species and provide the only useful key. However, the genus is in need of revision.

Hyperoche mediterranea Senna

Fig.12

Hyperoche mediterranea Senna, 1908: 159-168, figs 1-10, pl.1 figs 1,2.

Material examined. 1 male (5.6 mm) from station JP 72-23 (AM P39776).

Diagnosis. Epimeral plates with rounded margins distally. Gnathopod 1, article 4 posterodistal corner produced, almost reaching proximal margin of article 6. Gnathopods 1 and 2, dactyl attached terminally in normal manner; carpal process as long or slightly longer than article 6. Pereopods 3-7, all articles with covering of fine setae, especially articles 4-6. Telson length about half peduncle of uropod 3.

Remarks. *Hyperoche mediterranea* is readily distinguished by the form of the gnathopods and the posteriorly rounded epimeral plates. The only congener with rounded epimeral plates is *H. martinezi* (Müller, 1864) in which the posterodistal corner of article 4 of gnathopod 1 is only slightly produced.

Hyperoche mediterranea seems to be a shallow water species (Hurley, 1955) and this is supported by the present finding.

Distribution. A relatively rare species known from widely separated records in temperate regions but not yet recorded from the Indian Ocean. It is a new record for Australian waters although it has been recorded from New Zealand (Hurley, 1955).

Lestrigonus Milne-Edwards, 1830

Remarks. This genus has been revised by Bowman (1973) who provides a key and very useful illustrations for each species. Bowman recognised six species of which three are represented in the present collection. One other species, *L. macrophthalmus* (Vosseler, 1901), has previously been recorded from Australia (Zeidler, 1978).

Lestrigonus bengalensis Giles

Lestrigonus bengalensis Giles, 1887: 224-227, pls 6,7.
Hyperia dysschistus Stebbing, 1888: 1388-1391, pl.167.
Hyperia bengalensis.–Bovallius, 1889: 199-201.
Hyperia thoracica Bovallius, 1889: 233-236, pl.11 figs 37-41.
Hyperia gilesi Bovallius, 1889: 236-239.
Hyperia atlantica Vosseler, 1901: 67-70, pl.6 figs 5-15.

Material examined. 43 females (0.9-2.8 mm), 13 males (1.7-2.5 mm) from stations JP 89-2 (AM P39777 - 19 f, 1 m) and JP 89-3 (AM P39778 - 20 f, 8 m; SAM C4209 - 4 f, 3 m).

Diagnosis. Pereonites 1-5 fused in female, 1-4 fused in male. Gland cone in female produced anteroventrally, extending anterior to and overlapping epistome, with rounded apex; in male a rounded lobe produced ventrally. Gnathopod 1, article 2 with strong bulge on anterior margin, more pronounced in female; article 4 with 2 posterodistal spines; article 5 with 1 or 2 spines on posterior margin and 3 on carpal process; article 6 with single spine medially on anterior margin. Gnathopod 2 similar to gnathopod 1 except carpal process distinctly spoon-shaped and produced to about middle of article 6. Pereopods 3 and 4, articles 4 and 5 with single posterodistal spine; articles 5 and 6 with comb of spinules on posterior margin. Pereopod 5 of female and pereopods 5-7 of male, article 6 with comb of spinules on anterior margin. Pereopods 5-7, article 6 with straight anterodistal spine overlapping dactyl.

Remarks. This species is one of the most distinctive of the genus easily recognised by the number of fused pereonites. Females are generally more robust than other

species of *Lestrigonus* and the number of fused pereonites is constant throughout the size range (Zeidler, 1978). Males mostly have pereonites 1 to 4 fused, but in juveniles, pereonites 1 to 5 may be fused and in some very large specimens the suture of pereonite 4 may be almost complete. Males of all other species of *Lestrigonus* however, have pereonites 1 to 2 fused (sometimes 1-3 in juveniles) and cannot be confused with *L. bengalensis*.

Three ovigerous females were captured at the first station and four at the latter; all about 2.0 mm in length.

Distribution. Very common in tropical waters worldwide, tending to occur in coastal waters. Previous records from Australian waters are by Bowman & McGuinness (1982), Dakin & Colefax (1940 – as *Hyperia hydrocephala*), Sheard (1965), Stebbing (1888

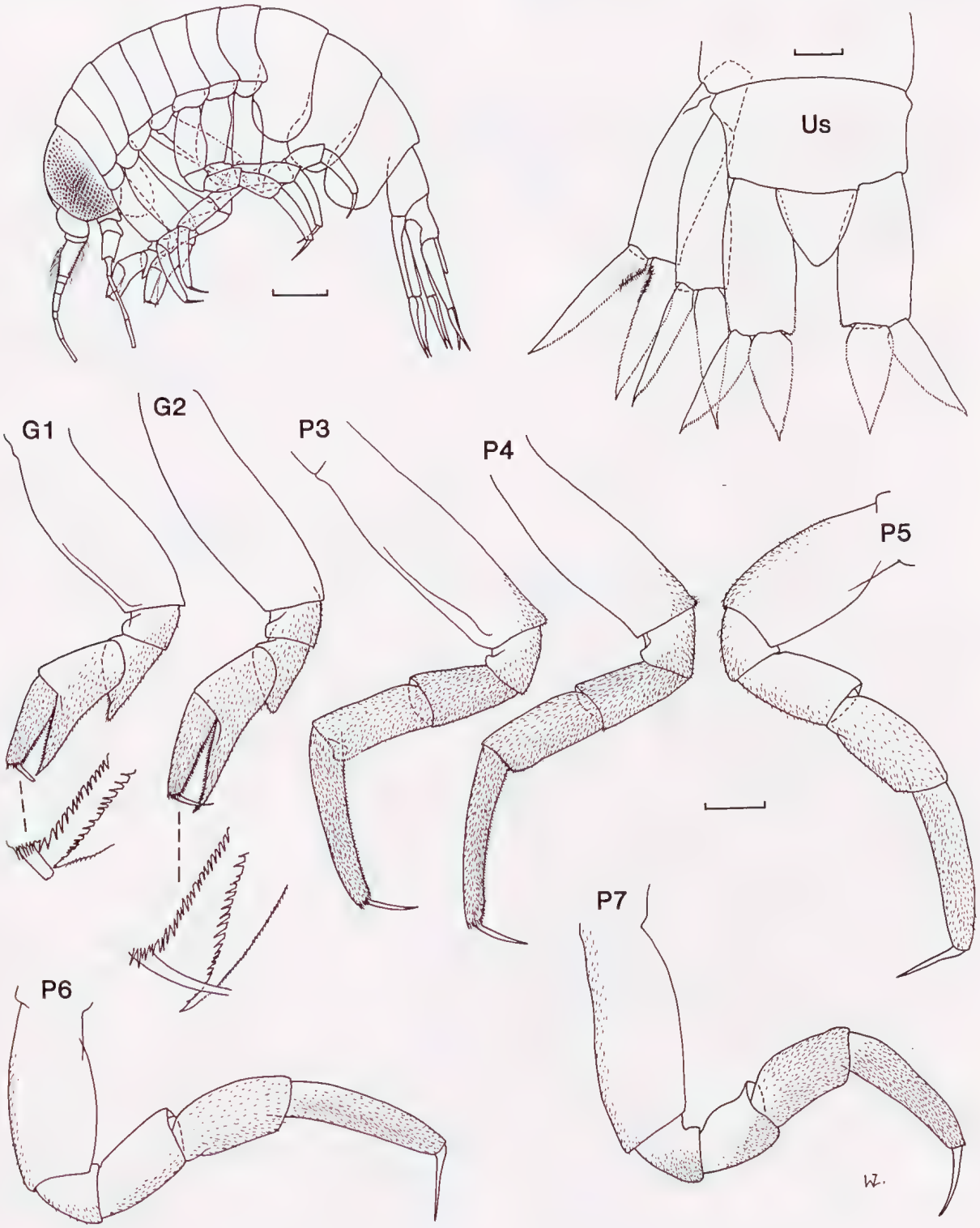

Fig.12. *Hyperoche mediterranea* Senna, male 5.6 mm (scales = 0.5 mm, 0.2 mm).

– as *Hyperia dysschistus*), Watson & Chaloupka (1982) and Zeidler (1978).

Lestrigonus crucipes (Bovallius)

Fig.13

Hyperia crucipes Bovallius, 1889: 225-228, pl.11 figs 14-25.

Material examined. 10 females (3.2-4.1 mm), 3 males (3.1, 3.8 and 4.5 mm) from station JP 72-23 (AM P39779 - 7 f, 2 m; SAM C4210 - 3 f, 1 m).

Diagnosis. Pereonites 1-3 fused in female, 1-2 fused in male. Gland cone obtuse, projecting obliquely anteroventrally; more produced in female than male. Gnathopod 1, article 4 with about 6 posterodistal spines; article 5 with 3 spines on posterior margin and 4 or 5

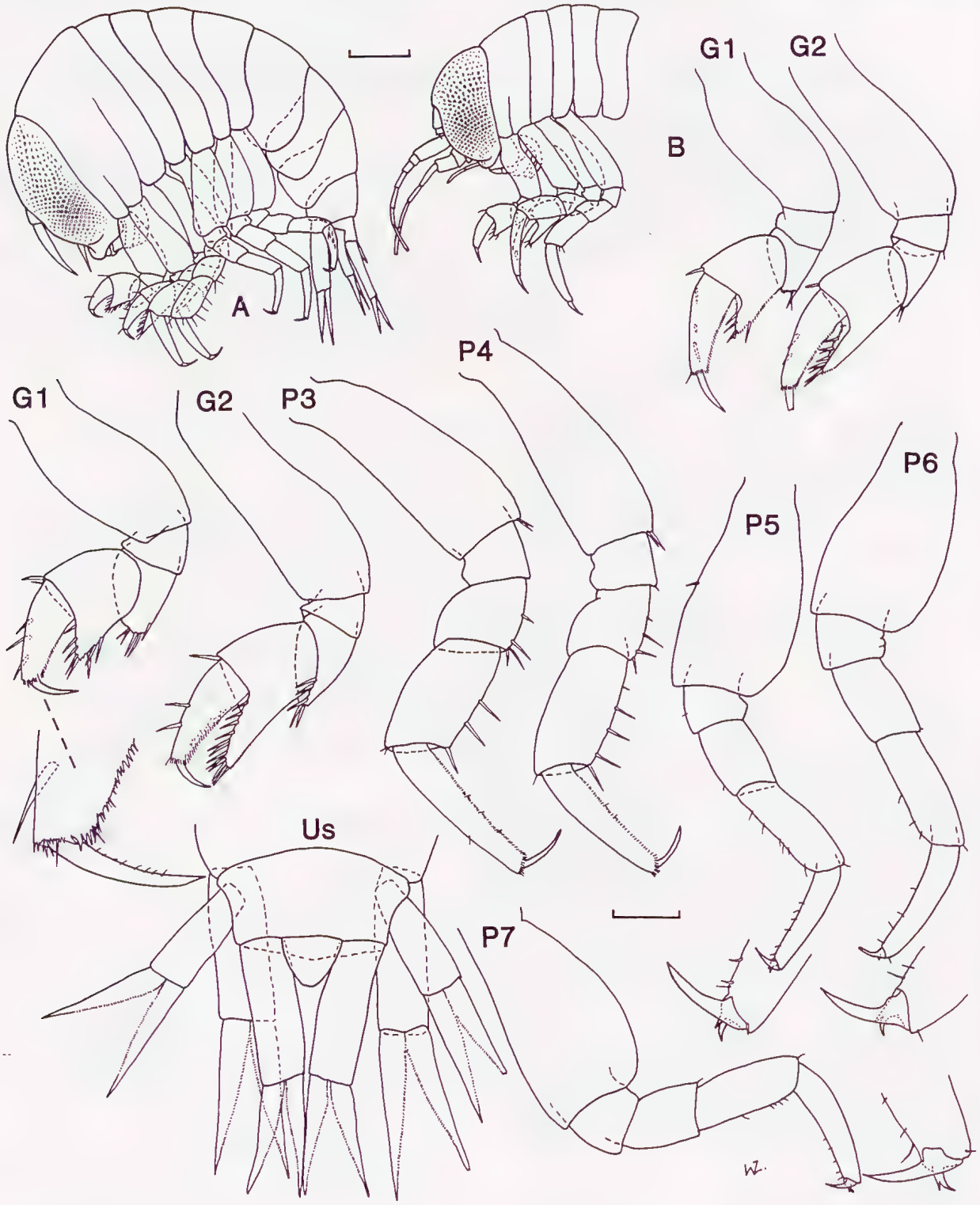

Fig.13. *Lestrigonus crucipes* (Bovallius). A, female 4.1 mm; B, male 4.5 mm (scales = 0.5 mm, 0.2 mm).

on carpal process; article 6 with 3 or 4 spines on anterior margin. Gnathopod 2, carpal process extended beyond midlength of article 6 and armed with several spines; article 6 with 2 or 3 spines on anterior margin. Pereopods 3 and 4, articles 4 and 5 with 3 or 4 spines on posterior margin; article 6 with close-set spinules on posterior margin. Pereopods 5-7, articles 5 and 6 with several short spines on anterior margin; article 6 produced distally into recurved, dentate hook overlapping dactyl medially.

Remarks. The present specimens agree with the description and figures given by Bowman (1973) except for the gnathopods which have the posterodistal corner slightly more produced, much like that illustrated by Bovallius (1889). An unusual feature of this species, which readily distinguishes it from all other congeners, is the recurved hook on the distal margin of article 6 of pereopods 5 and 7 which overlaps the dactyl on the medial side. In other features *L. crucipes* resembles *L. schizogeneios* (Stebbing, 1888), but in *L. schizogeneios* the gland cone is pointed and extends ventrally, nearly reaching the ventral margin of the buccal mass in males and extending just beyond in females; also the posterior margin of article 5 of pereopods 3 and 4 has only two spines.

All of the females were ovigerous.

Distribution. A relatively rare species known from a few records from warm regions of the Atlantic and Indian Oceans. It is a new record for Australian waters although Bowman & McGuinness (1982) recorded it in the north-eastern part of the Indian Ocean off Western Australia.

Lestrigonus schizogeneios (Stebbing)

Hyperia schizogeneios Stebbing, 1888: 1391-1394, pl.168.
Hyperia promontorii Stebbing, 1888: 1385-1387, pl.166B.
Hyperia zebui Stebbing, 1888: 1394.

Material examined. 1 female (2.4 mm) from station JP 89-2 (AM P39508).

Diagnosis. Pereonites 1-3 fused in female, 1-2 fused in male. Gland cone in female wedge-shaped, sharply pointed, extending beyond buccal mass; in male blunter, barely reaching ventral border of buccal mass. Gnathopod 1, article 4 with 2 or 3 posterodistal spines; article 5 with 2 spines on posterior margin and 3 or 4 on carpal process; article 6 with 2 or 3 spines on anterior margin. Gnathopod 2, carpal process produced to middle of article 6, armed with several spines; article 6 with 1 or 2 spines on anterior margin. Pereopods 3 and 4, article 5 with 2 spines on posterior margin; articles 5 and 6 with comb of spinules on posterior margin. Pereopods 5-7, articles 5 and 6 with comb of spinules on anterior margin. Pereopods 6 and 7 with simple spine on distal margin of article 6 overlapping dactyl medially.

Remarks. The number of fused pereonites can vary with maturity (Yang, 1960; Laval, 1968) and some specimens could then be confused with *L. bengalensis* or *L. macrophthalmus*. However, the wedge-shaped gland cone of *L. schizogeneios* is very distinctive and article 5 of pereopods 3 and 4 has two spines on the posterior margin (only one in *L. bengalensis* and *L. macrophthalmus*). The similarity of *L. schizogeneios* to *L. crucipes* has already been discussed under that species.

Distribution. Relatively common in tropical waters worldwide. Previous records from Australian waters are by Bowman & McGuinness (1982) and Dakin & Colefax (1940 – as *Hyperia promontorii*).

Themistella Bovallius, 1887

Remarks. Bowman (1973) revised this genus and considered it to be monotypic.

Themistella fusca (Dana)

Fig.14

Lestrigonus fuscus Dana,1853: 983, pl.67 fig.8a-c.
Hyperiella fusca.–Bovallius, 1887: 20.
Themistella steenstrupi Bovallius, 1887: 23.

Material examined. 1 ovigerous female (2.7 mm) from station JP 89-2 (AM P39780).

Diagnosis. Pereonites 1-5 fused in both sexes. Gland cone small. Gnathopod 1, article 4 with 3 posterodistal spines; carpal process about half length article 5 armed with 3 or 4 spines; article 6 with 1 spine on anterior margin. Gnathopod 2, carpal process extended beyond midlength of article 6 and armed with several spines; article 6 with 1 or 2 spines on anterior margin. Pereopods 3 and 4, articles 4 and 5 with 1 posterodistal spine. Pereopod 5 much longer than pereopods 6 and 7. Pereopods 6 and 7, dactyl with upward bend slightly distal to midlength. Telson very short, less than one quarter length peduncle of uropod 3.

Remarks. Bowman (1973) sorted out the past confusion concerning this species. The present specimen agrees in general with that figured by Bowman (1973) as *T. fusca* but differs slightly in that the suture of pereonite 5 is almost complete dorsally and the length of pereopod 7, relative to pereopod 6, is slightly shorter.

The relatively long pereopod 5, the short telson and the upward bend of the dactyls of pereopods 6 and 7 are characteristic features of this species.

Distribution. A relatively rare species, sparsely distributed in tropical waters of the world's oceans. First recorded from Australian waters (off North West Cape, Western Australia) by Bowman & McGuinness (1982).

PHRONIMIDAE

Phronima Latreille, 1802

Remarks. This genus has been adequately revised by Shih (1969) who also provides useful illustrations and a key to species. Additions and modifications have been made by Laval (1970) and Shih (1971a, 1971b, 1991)

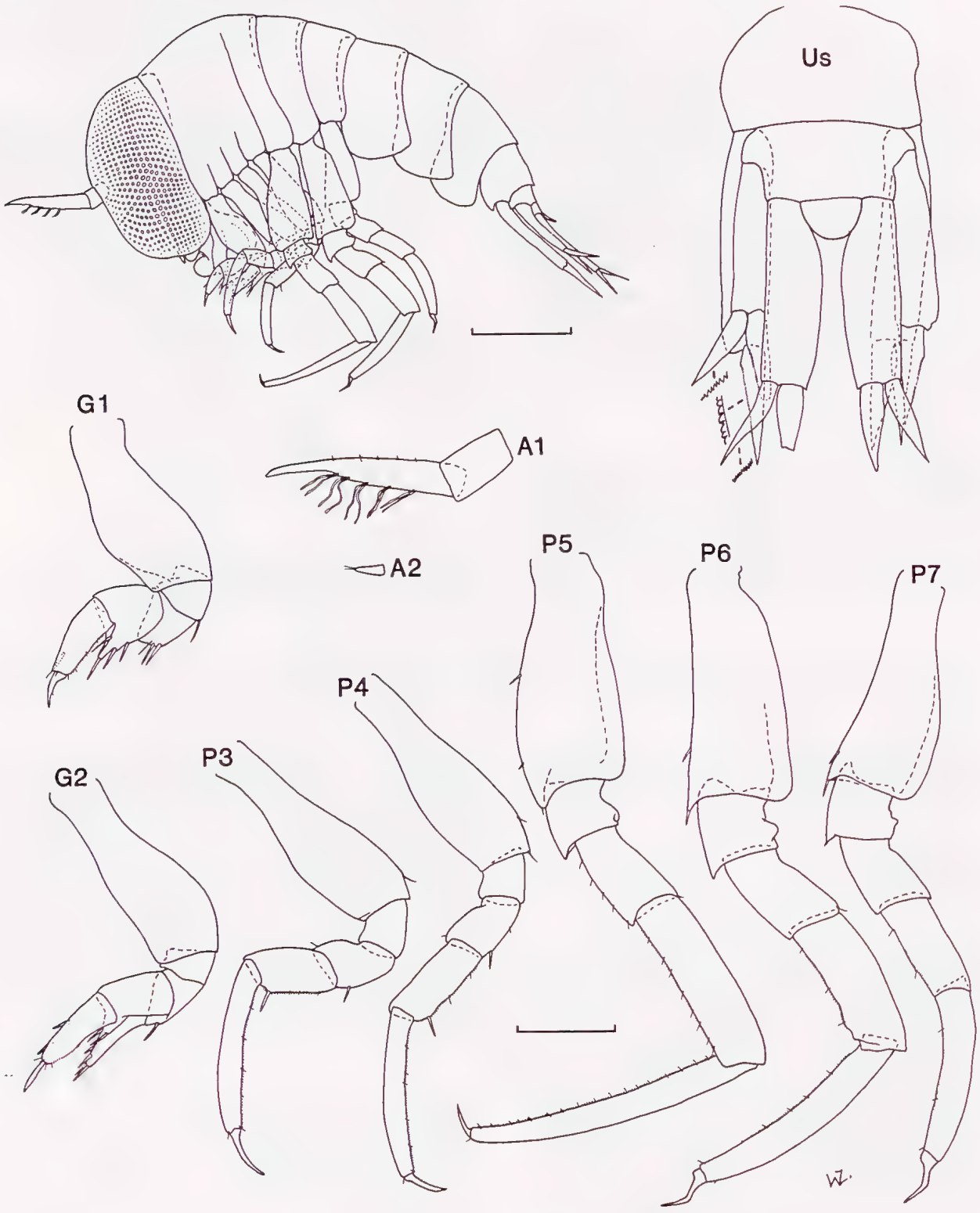

Fig.14. *Themistella fusca* (Dana), female 2.4 mm (scales = 0.5 mm, 0.2 mm).

resulting in the current recognition of ten species.

Phronima atlantica Guérin-Méneville

Phronima atlantica Guérin-Méneville, 1836: 7, pl.18 fig.1.

Material examined. 78 females (7.6-21.8 mm) and 1 male (7.0 mm) from stations JP 71-2 (AM P39781 - 4 f); JP 71-3 (AM P39782 - 51 f; SAM C4211 - 10 f); JP 71-4 (AM P39783 - 1 f); JP 71-7 (AM P39784 - 6 f); JP 71-8 (AM P39785 - 5 f); JP 72-23 (AM P39786 - 1 f) and JP 89-3 (AM P39510 - 1 m).

Diagnosis. Antenna 2 of male well developed with flagellum of 11-12 articles. Pereopod 5 longer than any other pereopod; articles 4 and 5 a little longer than wide; article 5, posterior margin evenly convex, anterior margin relatively straight, produced into large tooth almost extending beyond article 6 in females and a little further in males, distal margin with bifid tubercle, weaker than anterior tooth, with 4 or 5 tooth-like projections on posterior margin; article 6 extends well beyond anterior margin of article 5.

Remarks. Females of this species can be confused with *P. sedentaria* (Forskål, 1775) especially when dealing with juvenile specimens. However, in *P. sedentaria* the pleonites possess a posterodistal spinose process which is absent in *P. atlantica*. It may also be confused with juvenile *P. solitaria* Guérin-Méneville, 1836, which prior to Shih's (1969) revision, was considered to be a variety of *P. atlantica*. However, in *P. solitaria* the anterior margin of the carpus of pereopod 5 is distinctly convex just prior to the anterior tooth.

Distribution. A relatively common species widely distributed in tropical and temperate regions. Previous records from Australian waters are by Young & Anderson (1987) and Zeidler (1978).

Phronima colletti Bovallius

Phronima colletti Bovallius, 1887: 25.
Phronima diogenes Chun, 1889; 527-531, pl.3 figs 5,6.
Phronima gasti Dudlich, 1926: 134-137, figs 1-3.

Material examined. 2 females (8.8 and 10.2 mm) from station JP 71-8 (AM P39787).

Diagnosis. Antenna 2 of male well developed with flagellum of 12-13 articles. Pereopods 3 and 4 distinctly longer than pereopod 5. Pereopod 5, article 4 almost as wide as long with posterior bulge; article 5 rectangular with rounded posterior margin, almost as wide as long (wider in males), posteroproximal margin rounded, extended well above distal margin of article 4, anterior margin produced into large tooth extending beyond article 6, distal margin with bifid tubercle, much weaker than anterior tooth, with 3-4 tooth-like projections on posterior margin; article 6 does not extend beyond anterior margin of article 5.

Remarks. This species is closely related to *P. bucephala* Giles, 1887 but can most easily be distinguished from it by the form of pereopod 5. In *P. bucephala* article 4 is distinctly longer than wide and is not marginally overlapped posteriorly by article 5. Laval (1970) gives a full account of the differences between the two species. Males of *P. colletti* also closely resemble *P. pacifica* Streets, 1877, but in *P. pacifica*, article 4 of pereopod 5 is distinctly wider than long and article 5 is more trapezoid in shape.

Distribution. Widely distributed in tropical and temperate regions. Previous records from Australian waters are by Dakin & Colefax (1940), Sheard (1965) and Young & Anderson (1987).

Phronima curvipes Vosseler

Phronima curvipes Vosseler, 1901: 27-29, pl.3 figs 1-3.

Material examined. 2 females (9.9 and 11.6 mm) from stations JP 71-3 (AM P39788) and JP 72-23 (AM P39789).

Diagnosis. Antenna 2 of male well developed with flagellum of 7-9 articles. Pereopods 3 and 4 distinctly longer than pereopod 5. Pereopod 5, article 2, posterior margin reversed 'S' shape (more pronounced in females) with pointed posterodistal process; article 4 longer than wide in female, slightly wider than long in male, with distinct posterior bulge; article 5 in females, longer than wide with posteroproximal margin produced above distal margin of article 4, anterior margin produced into large tooth extending beyond article 6, distal margin with almost single (females) or bifid (males) tubercle, much weaker than anterior tooth, with 6-7 (females) or 4-5 (males), close tooth-like projections on posterior margin; article 6 just reaches (males) or extends beyond (females) anterior margin of article 5.

Remarks. Females of this species can resemble *P. solitaria* but are readily distinguished from this and other species of *Phronima* by the characteristic reversed 'S' curvature of the second article of pereopod 5. Males are most similar to *P. colletti* and *P. pacifica* but can be distinguished by the details in the shape of pereopod 5 and by the number of flagella articles of antenna 2 (see diagnoses).

Distribution. A relatively uncommon species widely distributed in tropical and temperate regions. First recorded from Australian waters by Young &

Anderson (1987).

Phronima pacifica Streets

Phronima pacifica Streets, 1877: 128-130.

Material examined. 7 females (3.3-10.4 mm), 3 males (7.2, 8.8 and 9.0 mm) from stations JP 71-2 (AM P39790 - 1 m); JP 71-3 (AM P39791 - 3 f, 1 m; SAM C4212 - 1 f, 1 m); JP 72-23 (AM P39792 - 1 f); F43 (AM P39500 - 1 f) and JP 89-3 (AM P39509 - 1 f).

Diagnosis. Antenna 2 of male well developed with flagellum of 15-17 articles. Pereopods 3 and 4 distinctly longer than pereopod 5. Pereopod 5, article 4 a little wider than long with strong posterior bulge; article 5 wider than long with posterior margin strongly dilated proximally and laterally, anterior margin produced into large tooth extending beyond article 6, distal margin with bifid tubercle, much weaker than anterior tooth with 4 or 5 tooth-like projections on posterior margin, of which, the first can be slightly isolated from the rest; article 6 just reaches (males) or extends slightly beyond (females) anterior margin of article 5.

Remarks. The female of this species is easily distinguished from its congeners by the shape of pereopod 5. Males closely resemble *P. colletti* and in the past have been confused with it (Shih, 1969). The similarity of males to *P. colletti* and also *P. curvipes* is discussed under those species.

Distribution. Widely distributed in tropical and subtropical regions. Previous records from Australian waters are by Sheard (1965), Young & Anderson (1987) and Zeidler (1978).

Phronima sedentaria (Forskål)

Cancer sedentarius Forskål, 1775: 95-96.
Gammarus sedentarius.–Schousboe, 1802: 11, figs 1-6.
Phronima sedentaria.–Latreille, 1803: 291.
Phronima custos Risso, 1816: 121, pl.2 fig.3.
Phronima borneensis Bate, 1862: 318, pl.51 fig.3.
Phronima novaezealandiae Powell, 1875: 294, pl.21 figs 1,2.
Phronima spinosa Bovallius, 1887: 25.
Phronima tenella Stebbing, 1888: 1354-1356, pl.161A.
Phronima affinis Vosseler, 1901: 20, pl.1 figs 12-16.

Material examined. 204 females (8.0-29.6 mm) from stations JP 71-2 (AM P39793 - 8 f); JP 71-3 (AM P39794 - 40 f; SAM C4213 - 10 f); JP 71-4 (AM P39795 - 3 f); JP 71-7 (AM P39796 - 31 f); JP 71-8 (AM P39797 - 10 f); JP 72-23 (AM P39798 - 3 f); K 72-07-01 (AM P39799 - 1 f); K 73-01-11 (AM P39800 - 2 f); K 74-05-01 (AM P 39801 - 10 f); JP 77-17 (AM P39802 - 3 f); JP 77-18 (AM P 39803 - 14 f); JP 77-19 (AM P39804 - 13 f); JP 77-25 (AM P39805 - 18 f); JP 77-26 (AM P39806 - 18 f); JP 77-27 (AM P39807 - 4 f); JP 77-28 (AM P39808 - 15 f); JP 89-2 (AM P39809 - 1 f).

Diagnosis. Antenna 2 of male, rudimentary. Pleonites with spinose posterodistal process. Pereopods 3 and 4 shorter than pereopod 5 in females, longer in males. Pereopod 5, articles 4 and 5 much longer than wide; article 5, anterior margin in females produced into large tooth extending well beyond article 6 in mature specimens, in males weakly developed, often shorter than carpal tubercle sometimes extending just beyond article 6 in mature females with 6 or 7 tooth-like projections on posterior margin; article 6 extended well past anterior margin of article 5 with median tubercle on anterior or dorsal margin in mature females.

Remarks. This was by far the most common species of *Phronima* in the present collections. Only one female from station JP 89-2 (April) was ovigerous.

The similarity of *P. sedentaria* to *P. atlantica* and *P. solitaria* is discussed under those species.

Distribution. A common species widely distributed in tropical and temperate regions. Previous records from Australian waters are by Guiler (1952), Shih (1969, Dana Stn 3663), Stebbing (1888) and Young & Anderson (1987).

Phronima solitaria Guérin-Méneville

Phronima solitaria Guérin-Méneville, 1836: 7, pl.18 fig.1.
Phronima custos Bate, 1862: 318, pl.51 fig.2.
Phronima megalodous Stebbing, 1888: 1353-1354, pl.162A.
Phronima atlantica var. *solitaria*.–Vosseler, 1901: 23, pl.2 fig.5.

Material examined. 4 females (15.4-19.2 mm) from stations JP 71-3 (AM P39810 - 2 f; SAM C4214 - 1 f) and JP 72-23 (AM P39811 - 1 f).

Diagnosis. Antenna 2 of male moderately developed with flagellum of up to 9 articles. Pereopods 3 and 4 shorter than pereopod 5 in females, longer in males. Pereopod 5, articles 4 and 5 much longer than wide; article 5, anterior margin in females produced into large tooth extending well beyond article 6 especially in mature specimens, in males weakly developed, sometimes shorter than carpal tubercle; distal margin with bifid tubercle in juvenile females and males, in mature females, single, projected beyond article 6 with 7-9 tooth-like projections on posterior margin; article 6 extended well past anterior margin of article 5 with very weak tubercle on anterior or dorsal margin.

Remarks. Prior to Shih's (1969) revision of the family, this species was considered to be just a variety

of *P. atlantica*. Although *P. solitaria* is very similar to *P. atlantica* and to *P. sedentaria* it is "easily distinguished from *P. atlantica* by the shape of the carpus of pereopod 5, and from *P. sedentaria* by the much larger length ratio of the 7th pereon segment to the 1st pleon segment" (Shih, 1969: 17).

Distribution. A relatively rare species known from widely separated records mainly in tropical regions. First recorded from Australian waters by Young & Anderson (1987).

PHROSINIDAE

Anchylomera Milne Edwards, 1830

Remarks. This distinctive genus is considered to be monotypic.

Anchylomera blossevillei Milne Edwards

Anchylomera blossevillei Milne-Edwards, 1830: 394.
Anchylomera hunterii Milne-Edwards, 1830: 394.
Hieraconyx abbreviatus Guérin-Méneville, 1836: 5, pl.17 fig.2,2a-f.
Cheiropristis messanensis Natale, 1850: 8, pl.1 fig.2.
Anchylomera purpurea Dana, 1853: 1001, pl.68 fig.9a-m.
Anchylomera thyropoda Dana, 1853: 1004, pl.68 fig.10.
Anchylomera antipodes Bate, 1862: 322-323, pl.51, figs 9,10.

Material examined. 457 females (3.0-8.3 mm), 235 males (6.5-9.1 mm) from stations JP 71-2 (AM P39812 - 13 f, 1 m); JP 71-3 (AM P39813 - 415 f, 212 m; SAM C4215 - 20 f, 20 m); JP 71-4 (AM P39814 - 1 f); JP 71-8 (AM P39815 - 1 f) and JP 72-23 (AM P39816 - 7 f, 2 m).

Diagnosis. Head globular. Pereonites 1 and 2 fused. Pereopods 3 and 4 subchelate. Pereopod 5 longer than any other pereopod with very broad articles; article 5, distal margin with short, rounded teeth forming perfect folding hand with article 6. Pereopod 6 prehensile with dilated article 5. Pereopod 7 reduced to basis and at least 2 additional articles, sometimes complete.

Remarks. This was the most abundant species of Hyperiidae in the collections. Many of the females were ovigerous, usually at about 7.0 mm (JP 71-2, 71-3, 71-4).

Distribution. A common, cosmopolitan species favouring tropical and temperate regions. Previous records from Australian waters are by Dakin & Colefax (1940), Sheard (1965), Stebbing (1888), Watson & Chaloupka (1982), Young & Anderson (1987) and Zeidler (1978).

Phrosina Risso, 1822

Remarks. This distinctive genus is considered to be monotypic.

Phrosina semilunata Risso

Phrosina semilunata Risso, 1822: 245.
Dactylocera nicaeensis Milne Edwards, 1830: 393.
Phrosina longispina Bate, 1862: 320-321, pl.51 fig.7.
Phrosina pacifica Stebbing, 1888: 1430.
Phrosina australis Stebbing, 1888: 1431.

Material examined. 76 females (4.0-22.4 mm), 6 males (6.3-6.7 mm) from stations JP 71-2 (AM P39817 - 3 f, 2 m); JP 71-3 (AM P39818 - 36 f, 1 m; SAM C4216 - 10 f, 1 m); JP 71-4 (AM P39819 - 1 f); JP 71-8 (AM P39820 - 12 f, 2 m); JP 72-23 (AM P39821 - 10 f); JP 77-19 (AM P39822 - 3 f) and JP 89-7 (AM P39507 - 1 f).

Diagnosis. Head produced into 2 sharp, triangular, rostral points. Pereonites 1 and 2 fused. Pereopods 3 and 4 subchelate with large tooth-like carpal processes. Pereopod 5 broader and longer than any other pereopod; article 5, anterodistal margin with large tooth-like processes forming folding hand with article 6; article 6, dactyl-like, much longer than article 5. Pereopod 6 similar but much smaller than pereopod 5. Pereopod 7 reduced to broad basis and sometimes 1 additional, tiny article.

Remarks. About 16 ovigerous females (at an early stage), all around 18 mm in length, were captured in March (JP 71-3, 71-4).

Distribution. A common, cosmopolitan species favouring tropical and temperate regions. Previous records from Australian waters are by Guiler (1952), Sheard (1965), Stebbing (1888), Watson & Chaloupka (1982), Young & Anderson (1987) and Zeidler (1978).

Primno Guérin-Méneville, 1836

Remarks. This genus has been revised by Bowman (1978) who recognised four species previously lumped as *P. macropa* Guérin-Méneville, 1836. Two additional species have since been recognised, one by Bowman (1985) and the other by Sheader (1986).

Primno latreillei Stebbing

Primno latreillei Stebbing, 1888: 1445-1447, pl.179A.

Material examined. 60 females (3.4-10.0 mm), 8 males

(3.8-6.2 mm) from stations JP 71-2 (AM P39823 - 11 f, 2 m); JP 71-3 (AM P39824 - 1 f); JP 71-7 (AM P39825 - 11 f, 2 m); JP 71-8 (AM P39826 - 20 f, 2 m; SAM C4217 - 5 f, 1 m); JP 72-23 (AM P39827 - 11 f, 1 m) and JP 89-2 (AM P39828 - 1 f).

Diagnosis. Head with short, pointed rostrum. Pereopod 5, article 2 almost 3 times as long as broad; article 5 with longer teeth on anterior margin nearly as long as article is wide, proximal tooth long. Pereopod 6, article 6 with smooth margins.

Remarks. The present material agrees with the description and figures given for *P. latreillei* by Stebbing (1888) and Bowman (1978) particularly in the shape of article 2 of pereopod 7. However, there is considerable variation in the relative length of article 2 of pereopod 7 compared to the remaining articles combined, ranging from slightly longer to about twice as long. This brings the specimens within the morphological range of the closely related species, *P. johnsoni* Bowman, 1978 which, at least in Australian waters, is probably synonymous with *P. latreillei*. Vinogradov *et al.* (1982) regard *P. johnsoni* as a junior synonym of *P. latreillei*.

Ten ovigerous females ranging in size from 4.6-10.0 mm were captured in March (JP 71-2, 71-7, 71-8) and August (JP 72-23).

Distribution. Difficult to ascertain due to past confusion with *P. macropa* but Bowman (1978) records it from the central North Pacific, south-east Gulf of Guinea, eastern Mediterranean and the Red Sea. Previous records from Australian waters are by Barnard (1931), Dakin & Colefax (1940), Guiler (1952 – as *Euprimno macropus*), Sheard (1965 – as *P. macropus*), Stebbing (1888), Watson & Chaloupka (1982), Young & Anderson (1987 – as *P. johnsoni*) and Zeidler (1978 – as *P. macropa*).

PRONOIDAE

Eupronoe Claus, 1879

Remarks. Species of *Eupronoe* are difficult to identify with certainty and the genus is in need of revision. Vinogradov *et al.* (1982) recognise four species and provide useful illustrations and a key (in Russian). However, they have not recognised *E. intermedia* Stebbing, 1888 as a species separate from *E. armata* Claus, 1879 (Tashiro, 1978).

Eupronoe armata Claus

Fig.15A

?*Pronoe brunnea* Dana, 1853: 1015, pl.69 fig.5.

Eupronoe armata Claus, 1879b: 28.

Eupronoe serrata Claus, 1887: 52, pl.14 figs 1-6 (plate captioned *E. armata*).

Material examined. 1 male (7.6 mm) from station JP 71-3 (AM P39829).

Diagnosis. Head, round in female, produced in male but with rounded tip. Body with dorsoventral, cuticular striations. Gnathopod 1, weakly subchelate; article 4 expanded distally, slightly wider than article 5; article 5 with rounded posterior margin, narrower distally than proximally (more expanded in male). Gnathopod 2 chelate; articles 4 and 5 about equal in width; carpal process rounded, extended one half to two thirds length article 6. Pereopod 5, article 2 with anterior margin slightly concave for distal two thirds. Pereopod 7, terminal article circular, about as wide as long.

Remarks. The present specimen agrees with the figures given for this species by Claus (1887). Judging from the available literature, females differ slightly from males in that article 5 of gnathopod 2 is much narrower proximally (e.g., Vinogradov *et al.*, 1982). This sexual dimorphism and the lack of adequate illustrations in the literature has led to past misidentifications. The record of *E. armata* by both Young & Anderson (1987) and Zeidler (1978) is probably *E. minuta* Claus, 1879 and is here discussed under that species.

Distribution. Reported from widely separated areas in the tropical and warm temperate Atlantic and Indian oceans (Tashiro, 1978). Previous records from Australia have been misidentifications.

Eupronoe intermedia Stebbing

Fig.15B,C

Eupronoe intermedia Stebbing, 1888: 1517-1519, pl.188.

Material examined. 5 females (4.4-4.8 mm), 6 males (4.2-5.3 mm) from stations JP 72-23 (AM P39830 - 3 f, 3 m; SAM C4218 - 1 f, 1 m); JP 89-3 (AM P39831 - 1 m); F19 (AM P39501 - 1 m) and F34 (AM P39505 - 1 f).

Diagnosis. Like *E. armata* except as follows. Head of female and male more pointed, ending in small beak. Gnathopod 2, article 5 slightly wider and longer. Pereopod 5, article 2 with anterior margin convex in females and straight or only slightly concave in males. Pereopod 7, terminal article oval, at least twice as long as wide.

Remarks. Tashiro (1978) demonstrated that, although closely related to *E. armata*, this is a distinct species. It is most readily distinguished from *E. armata* by the more pointed head which ends in a small beak and by

the elongate terminal segment of pereopod 7 (semicircular in *E. armata*). The male gnathopods agree with the illustrations given by Stebbing (1888) with article 5 of gnathopod 1 approaching that of *E. maculata* Claus, 1879. The female gnathopods are very similar to *E. armata*. As with the previous species a failure to appreciate the sexual dimorphism, combined with a lack of adequate illustrations in the literature, has led to past misidentifications.

This is the first time that this species has been recognised from Australian waters although I have re-examined the specimens identified as *E. maculata* by Zeidler (1978) and have concluded that they represent *E. intermedia*. The specimen of *E. maculata* illustrated

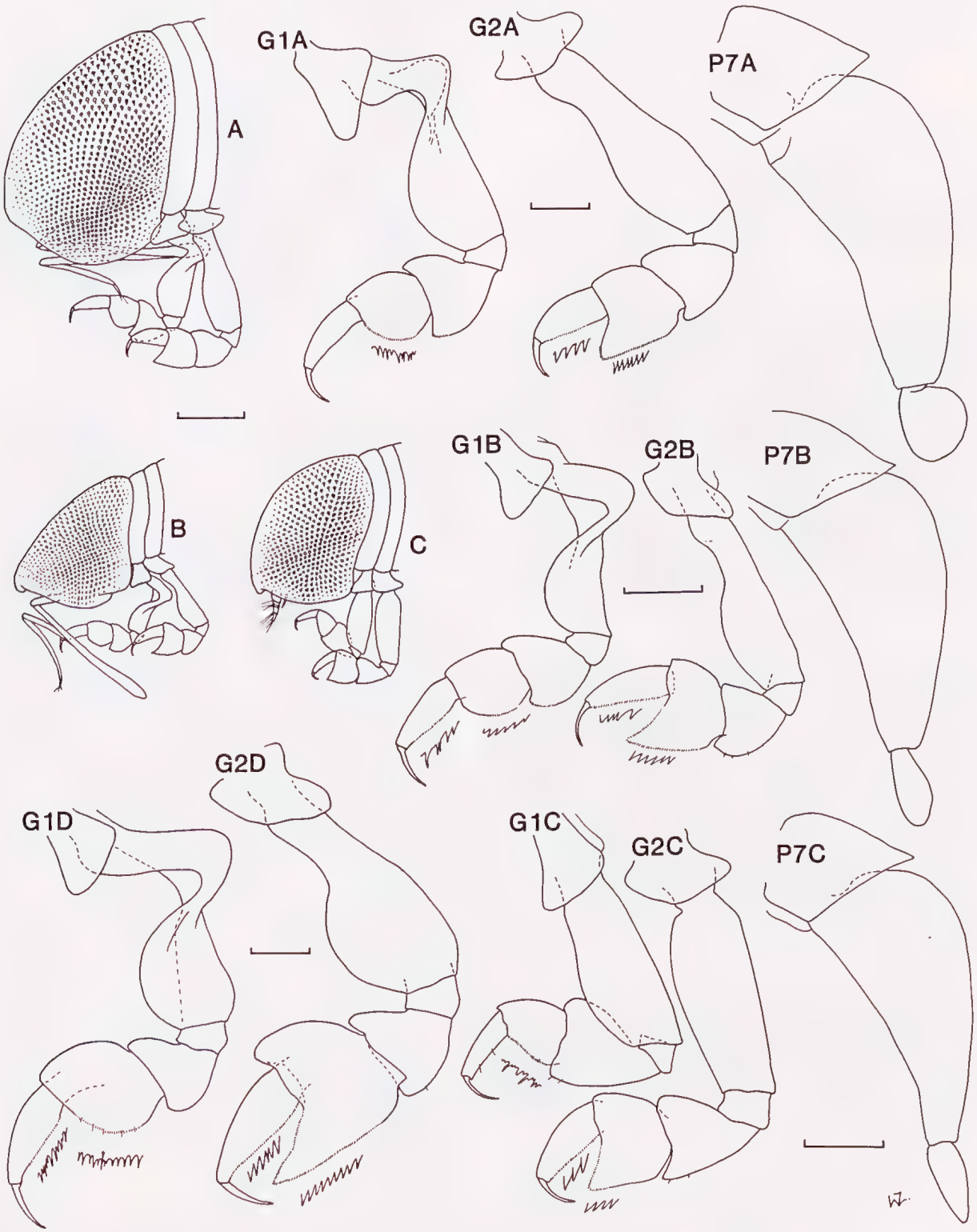

Fig.15. *Eupronoe* species. A, *E. armata* Claus, male 7.6 mm; B, *E. intermedia* Stebbing, male 5.3 mm from station JP 72-23; C, *E. intermedia*, female 4.8 mm from station JP 72-23; D, *E. maculata* Claus, male 9.7 mm (scales = 0.5 mm, 0.2 mm).

by Dakin & Colefax (1940) is also most likely this species.

One female from station F34 (May) was ovigerous.

Distribution. Tropical and warm temperate regions of the Atlantic Ocean, off South Africa and the Caribbean Sea (Tashiro, 1978).

Eupronoe maculata Claus

Fig.15D

Eupronoe maculata Claus, 1879b: 28.
Eupronoe inscripta Stebbing, 1888: 1510-1513, pl.187.

Material examined. 1 male (9.7 mm) from station JP 71-2 (AM P39832).

Diagnosis. Head, round in female, produced in male but with rounded tip. Body with dorsoventral, cuticular striations. Gnathopod 1 subchelate; article 4 expanded distally, distinctly narrower than article 5; article 5 expanded distally with relatively straight distal margin (slightly sloping with rounded posterodistal corner in male). Gnathopod 2 chelate; article 4 narrower than article 5; article 5 with anterodistal corner raised above, and slightly overlapping, article 6; carpal process almost as long as article 6. Pereopod 5, article 2 with convex anterior margin. Pereopod 7, terminal article oval, about twice as long as wide, sometimes slightly pointed terminally.

Remarks. The present specimen differs slightly from the illustrations given for this species by Claus (1887) in that the posterodistal process of article 5 of gnathopod 1 is more rounded, similar to that found in *E. armata* or *E. intermedia*. In females this process is usually more angular as illustrated by Bowman & Gruner (1973) and Vinogradov *et al.* (1982). *Eupronoe maculata* is best distinguished from the closely related species *E. intermedia* by gnathopod 1 in which article 5 is wider than article 4 and by gnathopod 2 in which the anterodistal process of article 5 extends almost to the limit of article 6.

Distribution. A relatively common species recorded from tropical and temperate regions. Previous records from Australia have been misidentifications (Dakin & Colefax, 1940; Zeidler, 1978) or the identification cannot be confirmed (Barnard, 1931; Sheard, 1965; Watson & Chaloupka, 1982).

Eupronoe minuta Claus

Fig.16

Eupronoe minuta Claus, 1879b: 28-29.
Eupronoe macrocephalata Bovallius, 1887: 41.
Eupronoe ornata Bovallius, 1887: 41.
Eupronoe pacifica Stebbing, 1888: 1513-1516.
Eupronoe atlantica Stebbing, 1888: 1519-1521.

Material examined. 1 ovigerous female (6.8 mm), 1 male (3.7 mm) from stations JP 71-4 (AM P39833 - 1 f) and F43 (AM P39834 - 1 m).

Diagnosis. Head of females large, rounded, as long as pereon; of males slightly pointed and smaller, as long as first 5 or 6 pereonites. Body with small semicircular cuticular markings. Gnathopod 1, article 4 expanded distally with small anterodistal and posterodistal lobe (larger in females) partly overlapping article 5; article 5 narrower than article 4 with small bulge on anterior margin and larger bulge on posterior margin (more distally in females) and straight distal margin. Gnathopod 2 chelate, article 4 similar to gnathopod 1 (especially of males); article 5 slightly wider than article 4, with anterodistal corner produced anteriorly to article 6, carpal process almost as long as article 6.

Remarks. The present specimen agrees with the figures given for the females of this species by Stephensen (1925) and Vinogradov *et al.* (1982). However, the gnathopods, particularly gnathopod 1, are quite unlike those illustrated for males of this species by Claus (1887), Chevreux & Fage (1925) and Stephensen (1925). According to Thurston (1976) large males agree with the illustrations of Claus but smaller specimens have gnathopod 1 closer to Stephensen's ?*E. minuta* (fig.56). Females on the other hand have gnathopod 1 more like the males when small, but become more like that illustrated here as the animal gets larger. However, I find it difficult to accept that in females article 5 of gnathopod 1 should become relatively smaller in size with growth. Whether or not those allometric changes actually take place cannot be determined here and require the examination of a large series of specimens, preferably from the same locality. If intermediate forms do not exist then the specimens as illustrated here may represent a species other than *E. minuta*.

I have re-examined the material identified as *E. armata* by Zeidler (1978) and all of the specimens agree with the illustrations of either Claus or Stephensen's ?*E. minuta*. The specimen of *E. armata* illustrated by Young & Anderson (1987) is like the present one and for the moment must be referred to *E. minuta*.

Eupronoe minuta is the only species of the genus with small semicircular sculpture markings on the body; the other four currently recognised species have quite distinct dorsoventral striations on the body and sometimes also on parts of the pereopods (Tashiro, 1978; Zeidler, 1978).

Distribution. Widely distributed in tropical and temperate regions. It is a new record for Australian waters although Stebbing (1888) recorded some specimens similar to *E. atlantica* (= *E. minuta*) from south of

Australia and Tranter (1977) recorded it from the north-eastern part of the Indian Ocean off Western Australia.

Parapronoe Claus, 1879

Remarks. This genus is in need of revision although the four currently recognised species (Vinogradov *et al.*, 1982) are more easily distinguished than species of *Eupronoe*.

Parapronoe campbelli Stebbing

Fig.17

Parapronoe campbelli Stebbing, 1888: 1522-1526, pl.189.

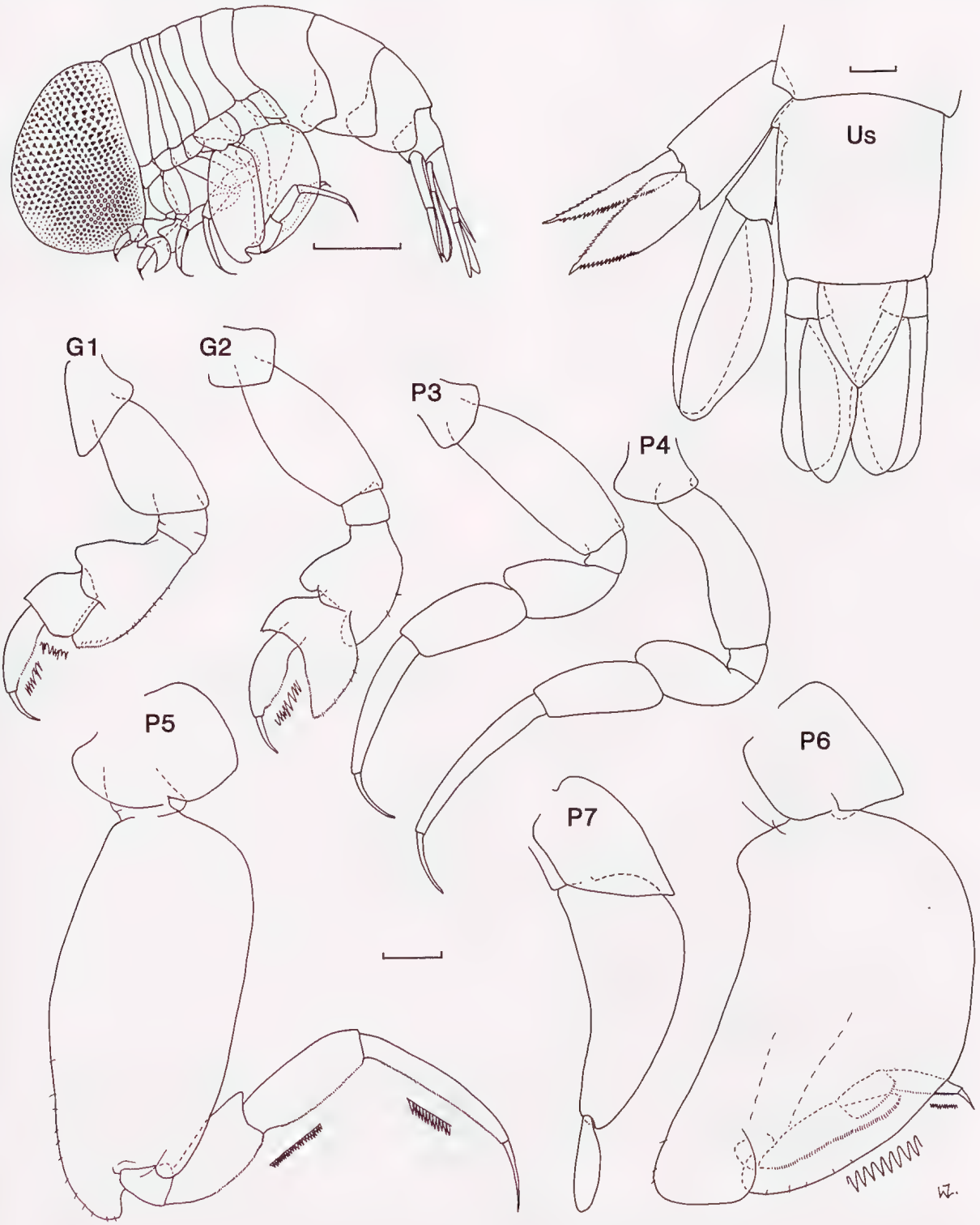

Fig.16. *Eupronoe minuta* Claus, female 6.8 mm (scales = 1.0 mm, 0.2 mm).

Material examined. 18 females (6.0-11.5 mm), 9 males (6.0-11.3 mm) from stations JP 71-2 (AM P39835 - 2 f, 2 m); JP 71-3 (AM P39836 - 6 f, 4 m; SAM C4219 - 2 f, 2 m); JP 71-4 (AM P39837 - 1 f); JP 71-7 (AM P39838 - 1 f); JP 71-8 (AM P39839 - 4 f); JP 72-23 (AM P39840 - 1 f, 1 m) and F33 (AM P39841 - 1 f).

Diagnosis. Head produced into rounded point in both sexes. Body with longitudinal cuticular pits or ridges. Epimeral plate 1 without posterodistal excavation. Gnathopod 1, article 5 with slightly convex posterior margin. Gnathopod 2, carpal process pointed, slightly longer than article 6. Pereopod 5, article 2 more than twice as long as wide. Uropod 3 rami lanceolate. Telson subequal in length to uropod 3, about three quarters length double urosomite.

Remarks. This species resembles *P. crustulum* and

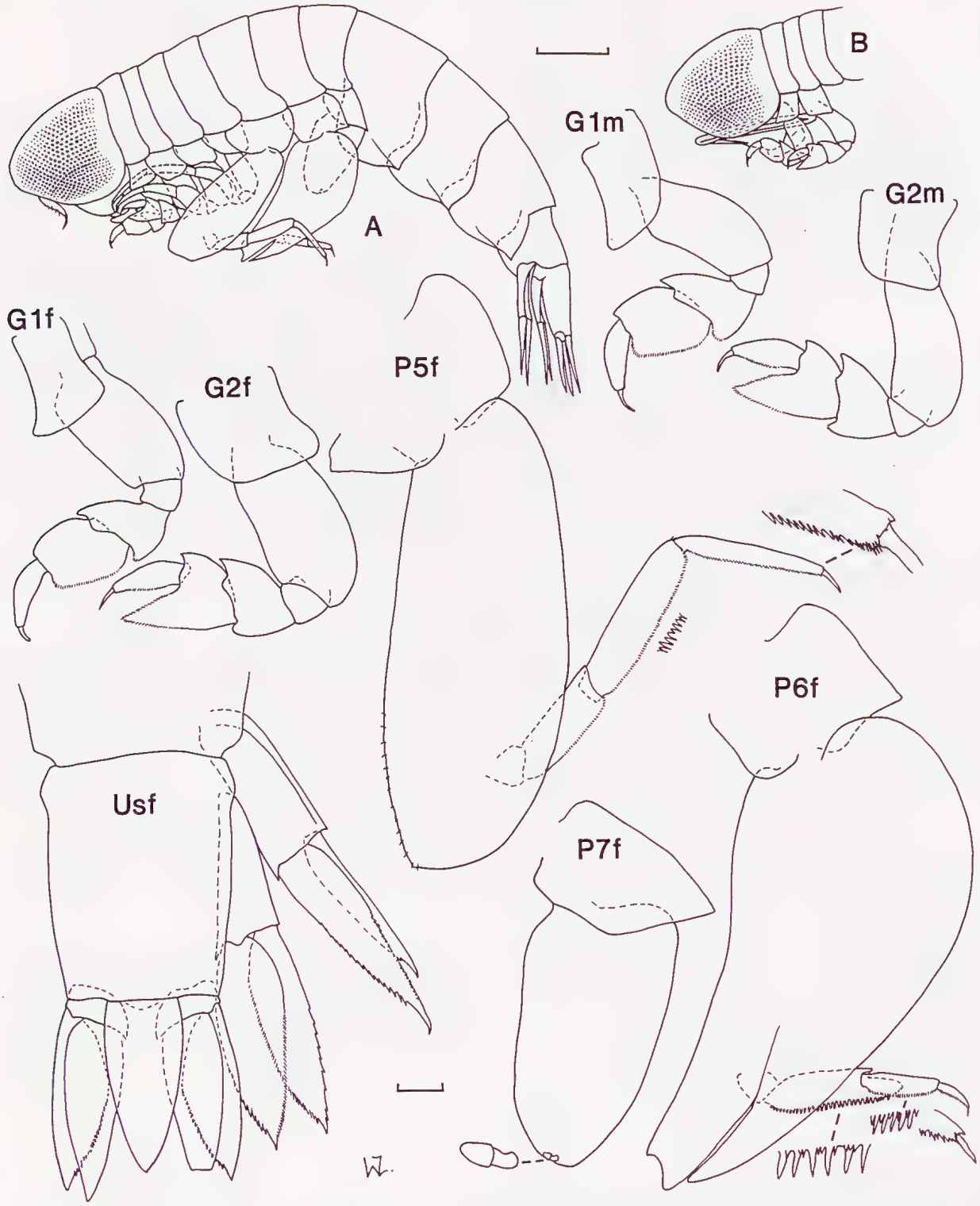

Fig.17. *Parapronoe campbelli* Stebbing, from station JP 71-3. A, female 10.7 mm; B, male 9.8 mm (scales = 1.0 mm, 0.2 mm).

in the past has been synonymised with it (e.g., Shoemaker, 1945). However, it is easily distinguished from all its congeners by the body markings which consist of longitudinal pits or ridges (circular in other species), the relatively more narrow second articles of pereopods 5 and 6 and in the females the head is not rounded but is pointed as in males. In addition, *P. crustulum* has a distinctive posterodistal excavation on the first epimeral plate (Fig.18), a feature which is not found in *P. campbelli*. The material illustrated by Young & Anderson (1987) as *P. crustulum* is regarded as a misidentification and represents this species.

This was the most abundant species of Pronoidae in the collections. Two ovigerous females (10.8 and 10.0 mm) were captured in March (JP 71-4 and 71-8).

Distribution. Difficult to ascertain due to past confusion with *P. crustulum* but it is probably widely distributed in tropical and temperate regions. It is a new record for Australian waters, although Tranter (1977) recorded it from the north-eastern part of the Indian Ocean off Western Australia.

Parapronoe crustulum Claus

Fig.18

Parapronoe crustulum Claus, 1879b: 31.
Parapronoe atlantica Bovallius, 1887: 42.
Parapronoe clausi Stebbing, 1888: 1526-1529, pl.190.
Parapronoe clausoides Stebbing, 1888: 1529-1530, pl.191.
Parapronoe similis Spandl, 1927: 219-220, fig.38.
Parapronoe stebbingi Spandl, 1927: 220-221, fig.39.

Material examined. 8 females (6.3-21.8 mm) from stations JP 71-2 (AM P39842 - 1 f); JP 71-4 (AM P39843 - 2 f); JP 71-7 (AM P39844 - 2 f; SAM C4220 - 1 f); JP 71-8 (AM P39845 - 1 f) and JP 77-18 (AM P39846 - 1 f).

Diagnosis. Head produced in males, more rounded in females. Body with circular, cuticular markings. Epimeral plate 1 with distinct posterodistal excavation. Gnathopod 1, article 5 with slightly concave posterior margin for distal half. Gnathopod 2, carpal process pointed, slightly longer than article 6. Pereopod 5, article 2 less than twice as long as wide. Uropod 3 rami lanceolate. Telson subequal in length to uropod 3, one half to two thirds length double urosomite.

Remarks. A distinctive character of this species is the concave posterior margin of article 5 of gnathopod 1, a feature particularly prominent in adults. In smaller specimens (e.g., AM P39842) this article has more convex margins and resembles *P. campbelli*. This character, often used in the past to separate the two species, is therefore unreliable. So too is the relative length of the telson to the double urosomite which in the present specimens is similar to that found in *P. campbelli* (about two thirds), whereas the illustrations of both Claus (1887) and Stebbing (1888) indicate a ratio of about one half.

Four ovigerous females (16.5-21.8 mm) were captured in March (JP 71.4, JP 71.7).

Distribution. A relatively uncommon species widely distributed in tropical and temperate regions. Previous records from Australian waters are by

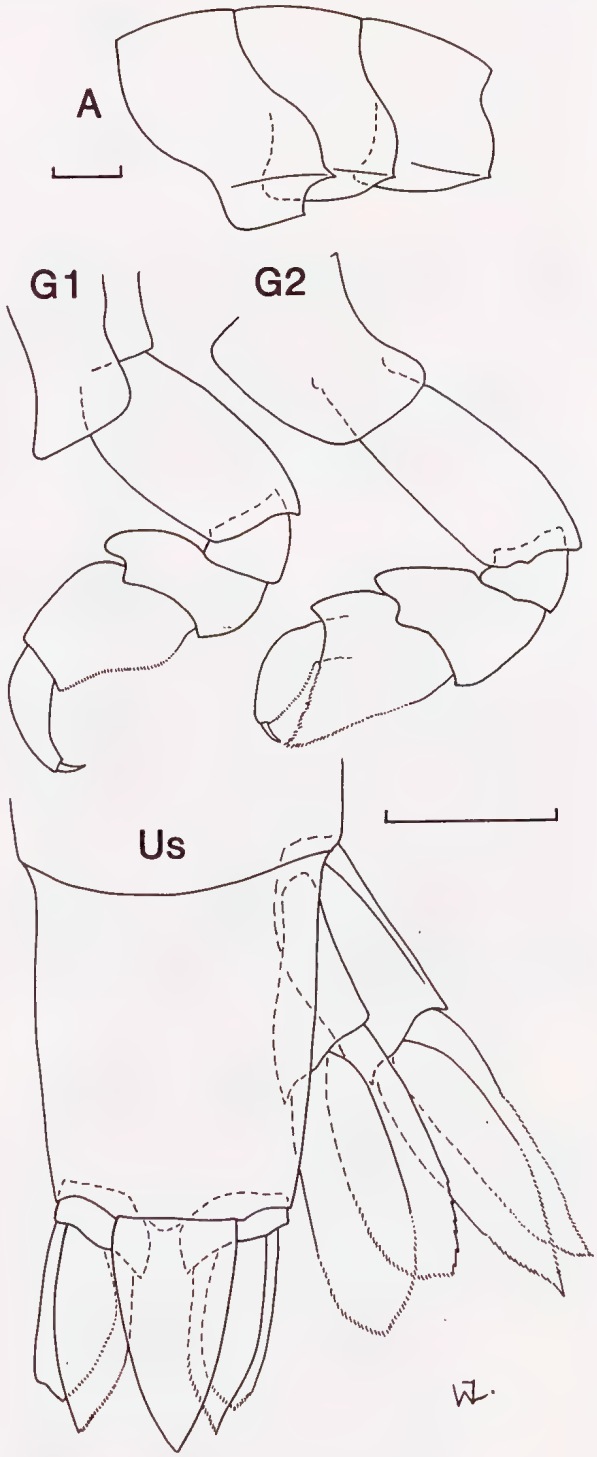

Fig.18. *Parapronoe crustulum* Claus, female 17.0 mm from station JP 71-8. A, lateral view of epimeral plates 1-3 (scales = 1.0 mm).

Guiler (1952) and Stebbing (1888 - as *P. clausi* and *P. clausoides*).

Parapronoe parva Claus

Parapronoe parva Claus, 1879b: 31.
Sympronoe parva Stebbing, 1888: 1533-1537, pl.192.
Sympronoe propinqua Stebbing, 1888: 1537, pl.193B.
Sympronoe var. *7-articulata* Stephensen, 1925: 162-163, figs 59-60.
Sympronoe anomala Shoemaker, 1925: 42-45, figs 14-15.
Sympronoe parva septemarticulata Pirlot, 1930: 33.

Material examined. 1 male (4.9 mm) from station JP 71-3 (AM P39847).

Diagnosis. Head produced in males, more rounded in females. Body with circular, cuticular markings. Epimeral plate 1 with small posterodistal excavation. Gnathopod 1, article 5 with straight or marginally concave posterior margin. Gnathopod 2, carpal process round, about half length article 6. Pereopod 5, article 2 less than twice as long as wide. Uropod 3, endopod oval-shaped, exopod bluntly pointed. Telson length about half uropod 3, about one quarter length double urosomite.

Remarks. This species is easily recognised by the form of the gnathopods and urosome. Stebbing (1888) erected the genus *Sympronoe* for this species and one other that he described as new at the time (now synonymous with *P. parva*). However, Semenova (1981), in describing a new species of *Parapronoe* (*P. elongata*) which had features in common with *Sympronoe*, concluded that the generic status of *Sympronoe* (considered monotypic) could not be maintained.

Distribution. Widely distributed in tropical and temperate regions. Previous records from Australian waters are by Barnard (1931), Young & Anderson (1987) and Zeidler (1978).

Pronoe Guérin-Méneville, 1836

Remarks. This relatively distinctive genus is considered to be monotypic.

Pronoe capito Guérin-Méneville

Pronoe capito Guérin-Méneville, 1836: 7, pl.17 fig.3.

Material examined. 1 female (12.4 mm) from station JP 71-3 (AM P39848), 1 male (11.6 mm) from station JP 71-2 (AM P39849).

Diagnosis. Antenna 2 of male short, folded only once or twice, unlike other Pronoidae. Gnathopods 1 and 2 simple with relatively broad articles, especially article 2 of gnathopod 1. Pereopod 5, article 2 not especially broad. Pereopod 6, article 2 oval, width about three quarters length. Uropods 2 and 3, endopod with rounded tip. Telson length about one third uropod 3.

Remarks. This species is easily distinguished by the gnathopods and by the unique structure of the second antennae of males.

Distribution. A relatively rare species, recorded mainly from tropical regions. It was first recorded from Australian waters by Young & Anderson (1987).

Brachyscelidae

Brachyscelus Bate, 1861

Remarks. This genus is in a state of considerable taxonomic confusion and a revision is long overdue. According to Madin & Harbison (1977) at least 17 species of *Brachyscelus* have been described but of these Vinogradov *et al.* (1982) recognise only four as valid. However, based on the present collection and published literature, I believe that *Brachyscelus* consists of at least five valid species. In trying to determine the specimens in the present collection I found it necessary to develop the following key which may be useful to others until a thorough revision of the genus is undertaken.

Key to the Species of *Brachyscelus*

1. Head round in males (like female); gnathopod 1, article 5 with anterodistal corner developed into feeble lobe; telson as long as wide 2

—— Head pointed in males; gnathopod 1, article 5 with anterodistal corner developed into distinct lobe partly overlapping article 6 (especially in mature specimens); telson longer than wide 3

2. Head length equivalent to first five segments of pereon or less; pereopod 6, anterior lobe article 2 with rounded distal margin; telson about as long as double urosomite ..... *B. globiceps* Claus

—— Head as long as pereon; pereopod 6, anterior lobe article 2 pointed; telson length about two thirds double urosomite ..... *B. macrocephalus* Stephensen

3. Pereopod 6, anterior lobe article 2 reaching well beyond article 3 with straight distal margin; double urosomite about as broad as long; uropod 3 with broad rami, particularly endopod ..... *B. crusculum* Bate

—— Pereopod 6, anterior lobe article 2 only reaching middle or limit of article 3 with round distal margin; double urosomite distinctly broader than long; uropod 3 with rami not especially broad 4

4. Gnathopods, article 5 with single row of large teeth; pereopod 7, articles 3-7 together equal in length to article 2; uropod 3, endopod slightly excised distally (as in *B. crusculum*); male antenna 2, article 5 very short ..... *B. rapax* Claus

—— Gnathopods, article 5 with large teeth interspersed with smaller ones; pereopod 7, articles 3-7 together shorter than article 2; uropod 3, endopod tapers gradually; male antenna 2, article 5 about half as long as article 4 ..... *B. rapacoides* Stephensen

Brachyscelus crusculum Bate

Fig.19

?*Orio zancleus* Natale, 1850: 12.
Brachyscelus crusculum Bate, 1861: 7-10, pl.2 figs 1-2.
Thamyris antipodes Bate, 1862: 335, pl.50 fig.4.
?*Thamyris lycaeoides* Claus, 1887: 60, pl.21 figs 1-2.
?*Thamyris mediterranea* Claus, 1887: 60, pl.15 figs 11-18.
Brachyscelus acuticaudatus Stebbing, 1888: 1555-1556, pl.197C.
Brachyscelus stebbingi Boone, 1935: 226-230, pls 67,68.

Material examined. 139 females (6.0-20.0 mm), 112 males (4.9-17.1 mm) from stations JP 71-2 (AM P39850 - 3 f, 3 m); JP 71-3 (AM P39851 - 94 f, 62 m; SAM C4221 - 20 f, 20 m); JP 71-4 (AM P39852 - 2 f, 5 m); JP 71-8 (AM P39853 - 4 f, 3 m); JP 72-23 (AM P39854 - 15 f, 8 m); JP 77-18 (AM P39855 - 1 f) and F19 (AM P39856 - 1 m).

Diagnosis. Head globular in females produced to rounded point in males. Antenna 2 of males, length terminal article slightly less than one third preceding article. Gnathopod 1, article 5 with anterodistal corner developed into lobe, partly overlapping article 6. Gnathopods 1 and 2, carpal process with large teeth with small serrations on margins. Pereopod 5, article 2, width almost twice length, with small anterodistal lobe partly overlapping article 3. Pereopod 6, article 2 with anterodistal lobe produced well beyond article 3, with straight distal margin. Double urosomite about as broad as long. Telson much longer than wide.

Remarks. In this species the head of males is pointed while that of females is rounded. However, recently moulted males, recognised by the antennae which are not fully developed, have a rounded head which becomes pointed later. Also the antennal pocket of the first gnathopods is not very noticeable in freshly moulted specimens but becomes deeper as the second antennae develop and the head becomes more pointed. These morphological changes during moulting and growth have probably contributed to past misidentifications of this and other species of *Brachyscelus*. Distinctive features of *B. crusculum* are: the shape of article 2, pereopod 6 which has a large anterodistal lobe with a straight distal margin and a smaller posterior lobe both of which almost cover article 3; the double urosomite which is about as long as it is broad, and the very broad endopod of uropod 3 which is especially broad in larger specimens.

Twenty of the females were ovigerous; most were captured in March (JP 71-3, 71-4), two in August (JP 72-23) and one in December (JP 77-18).

Distribution. A very common species, widely

distributed in tropical and temperate regions. Previous records from Australian waters are by Dakin & Colefax (1940), Guiler (1952), Sheard (1965), Young & Anderson (1987) and Zeidler (1978).

Brachyscelus globiceps (Claus)

Fig.20

?*Daira inaequipes* Dana, 1853: 993, pl.68 fig.5a-c.
Thamyris globiceps Claus, 1879b: 36-37.
Brachyscelus latipes Stebbing, 1888: 1550-1552, pl.197B.
Brachyscelus bovallii Stebbing, 1888: 1553-1555, pl.197A.

Material examined. 1 male (8.0 mm) from station JP 71-2 (AM P39857).

Diagnosis. Head globular in both sexes. Antenna 2 of males, length terminal article about one quarter preceding article. Gnathopod 1, article 5 with anterodistal corner developed into feeble lobe. Gnathopods 1 and 2, carpal process with large teeth with row of serrations or small teeth on margins. Pereopod 5, article 2, width two thirds length, without anterodistal lobe. Pereopod 6, article 3, with evenly rounded distal margin. Double urosomite, length about two thirds width. Telson about as long as wide.

Remarks. In this species the head of males is rounded like that of the females. It is very similar to *B. crusculum* but is most easily distinguished from it by the anterior lobe of article 2, pereopod 6 which is rounded and without a posterior lobe, and the double urosomite which is distinctly broader than long.

Distribution. A relatively rare species known from a few isolated records from the Arabian Sea (Barnard, 1937), Bermuda (Shoemaker, 1945), South West Africa (Barnard, 1932), Mediterranean (Stephensen, 1925), Zanzibar (Claus, 1879), Southern Pacific (Stebbing, 1888) and Great Barrier Reef (Barnard, 1931). The latter is the only previous record from Australian waters.

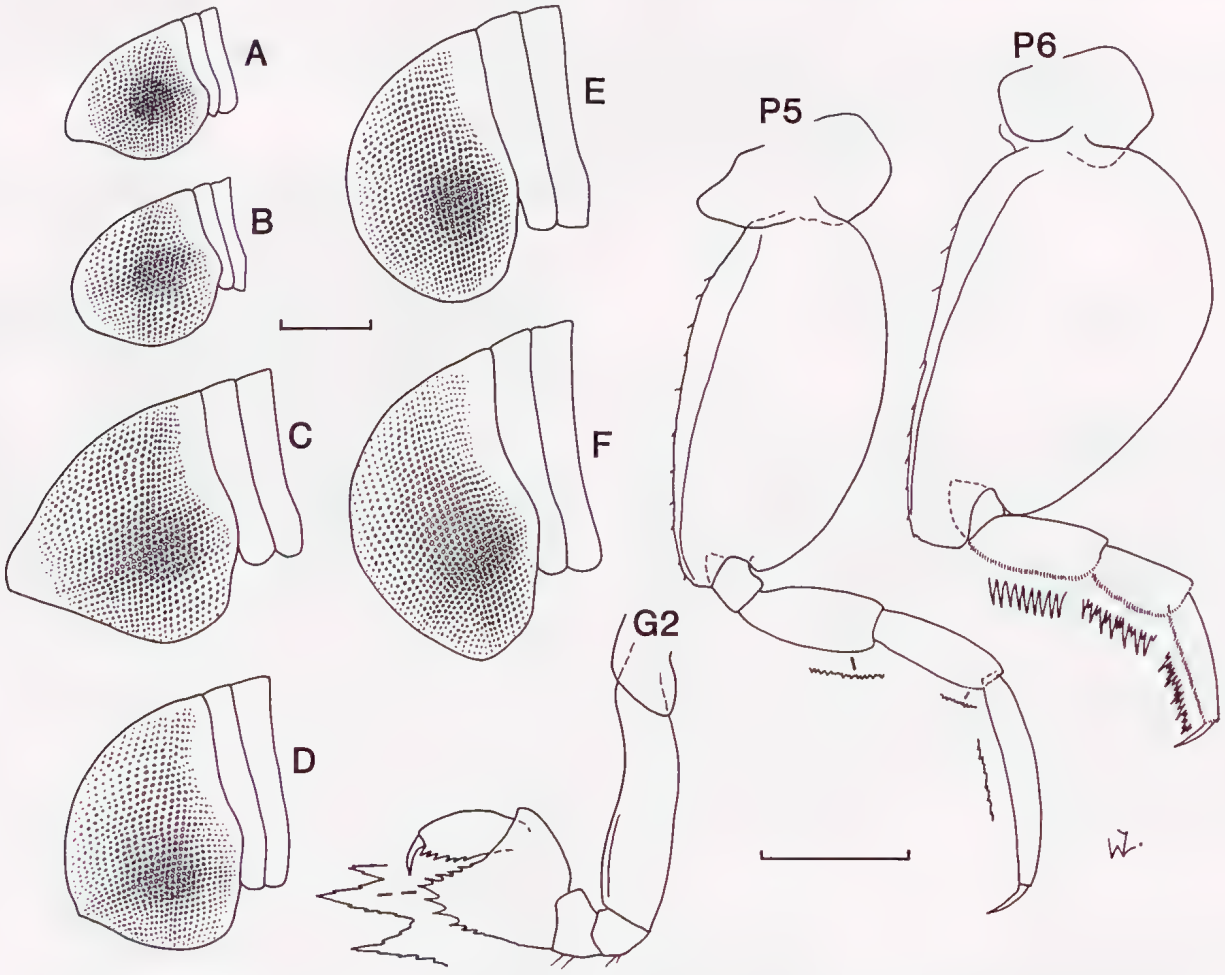

Fig.19. *Brachyscelus crusculum* Bate, variations in head shape. A, male 7.7 mm from station JP 72-23 with well-developed antennae; B, male 8.1 mm as above; C, male 17.0 mm from station JP 71-3 with well-developed antennae; D, male 11.9 mm from station JP 72-23, antenna with shortened and thickened articles (recently moulted); E, male 16.5 mm from station JP 71-3, antennae with shortened and thickened articles (recently moulted); F, female 16.8 mm from station JP 71-3. G2, P5, P6 from A (scales = 1.0 mm, 0.5 mm).

Brachyscelus rapacoides Stephensen

Fig.21

Brachyscelus rapacoides Stephensen, 1925: 179-180, figs 67-68.

Material examined. 1 male (5.9 mm) from station JP 72-23 (AM P39858).

Diagnosis. Head globular in females, produced to rounded point in males. Antenna 2 of males, length terminal article about half preceding article. Gnathopod 1, article 5 with anterodistal corner developed into distinct lobe, partly overlapping article 6. Gnathopods 1 and 2, carpal process with large teeth interspersed with 1 or 2 smaller teeth. Pereopod 5, article 2, width almost twice length, with very small anterodistal lobe. Pereopod 6, article 2 with anterodistal lobe produced to limit of

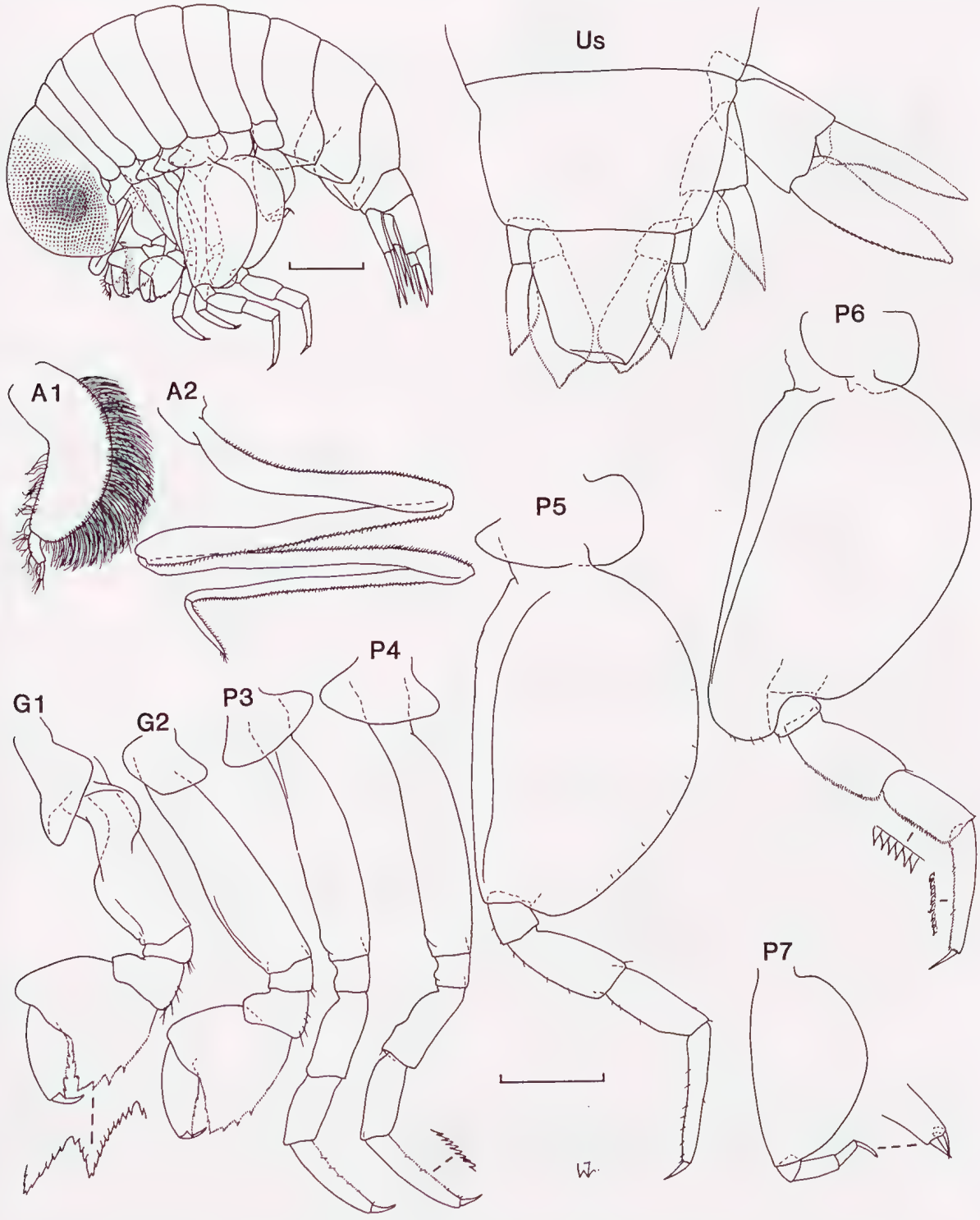

Fig.20. *Brachyscelus globiceps* (Claus), male 8.0 mm. A2 from right (scales = 1.0 mm, 0.5 mm).

article 3, with round, pointed distal margin. Double urosomite much wider than long. Telson much longer than wide.

Remarks. The present specimen agrees very well with the figures and description given for this species by Stephensen (1925). Vinogradov *et al.* (1982) consider it a synonym of *B. rapax* (Claus, 1879) but I believe that it is a valid species distinguished from *B. rapax* as illustrated by Claus (1887) by the following characters: i) male antenna 2, fifth article is about half as long as the fourth (very short in *B. rapax*); ii) gnathopod articles 5 and 6 have long teeth interspersed with one or two smaller ones (only serrations between large teeth in *B. rapax*); iii) pereopod 7, article 2 is much longer than remaining articles combined (about equal in *B. rapax*);

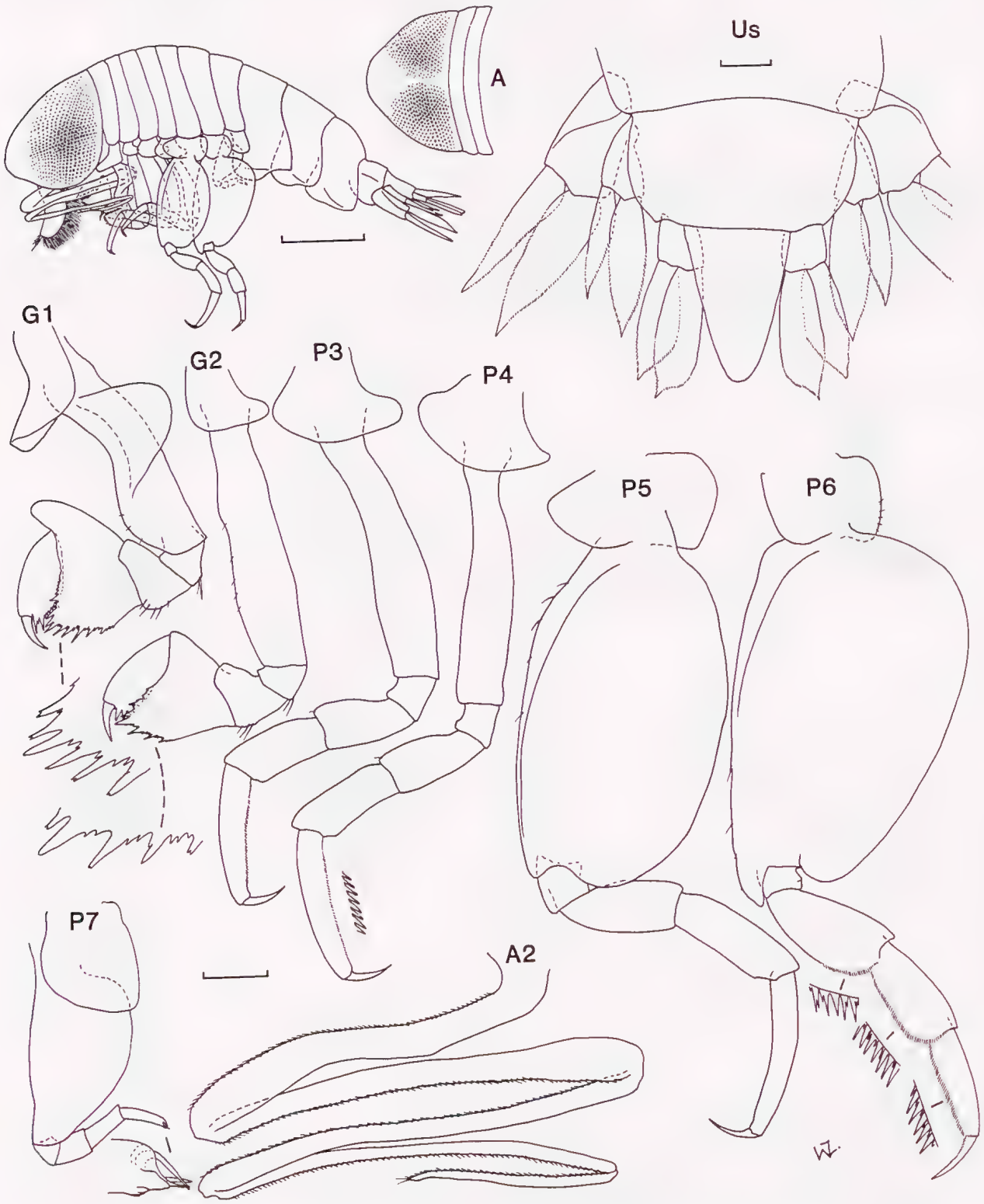

Fig.21. *Brachyscelus rapacoides* Stephensen, male 5.9 mm. A, dorsal view of head (scales = 1.0 mm, 0.2 mm).

and iv) telson is distinctly longer than wide (slightly longer than wide in *B. rapax*). The illustrations of *B. rapax* given by Vinogradov *et al.* (1982) appear to represent this species.

In the present specimen the eyes, when viewed dorsally, become widely separated anteriorly (Fig.21) unlike the previous two species in which the eyes are only separated by a narrow margin, almost to the tip of the rostrum. However, more material is required to determine whether or not this feature is of specific significance.

Distribution. Difficult to ascertain due to probably past misidentifications but according to Dick (1970) it is a rare species known from widely separated records in tropical and temperate regions. It is a new record for Australian waters although Vinogradov (1962) records it from south of Australia (45°26'S 125°52'E).

Euthamneus Bovallius, 1890

Remarks. This very distinctive genus is considered to be monotypic.

Euthamneus rostratus (Bovallius)

?*Daira debilis* Dana, 1853: 991, pl.68 fig.3.
Thamneus rostratus Bovallius, 1887: 31-32.
Thamneus platyrrhynchus Stebbing, 1888: 1558-1562, pl.198.
Thamneus recurvirostris Chevreux, 1900: 154-156, pl.18 fig.2.

Material examined. 2 females (3.9 and 7.9 mm), 1 male (7.1 mm) from station JP 72-23 (AM P39901).

Diagnosis. Head relatively small, with chisel-shaped rostrum. Body globular. Antenna 2, of males shorter than head, consisting of 4 articles arranged in zig-zag fashion. Pereopods 1-6 with numerous setae on distal articles. Gnathopods 1 and 2, carpal process with large teeth (like *Brachyscelus*). Pereopods 5 and 6, article 2 not markedly broadened. Telson slightly longer than wide, rounded terminally, distinctly shorter than uropod 3.

Remarks. This species is readily distinguished by the following suite of characters: the relatively small head with chisel-shaped rostrum; the dorsoventrally flattened globular body; the hexagonal markings on the surface of most appendages and the distinctive structure of the male second antenna. The second antenna of males is most unusual for Platysceloidea in that it consists of four shortened articles which are not folded under the head but arranged in a zig-zag fashion and together are much shorter than the head. In all other Platysceloidea, except Anapronoidae, at least some of the articles of the male second antenna are elongated and the entire appendage is neatly folded under the head and is much longer (often even when folded) than the head.

Whether or not this species should be placed in a separate family, based on the above characters, cannot be determined here but should it be warranted then Euthamneidae (Bovallius, 1890) should be resurrected.

Distribution. A relatively uncommon but widely distributed species known from records in tropical and temperate areas (Dick, 1970). The only previous record from Australian waters is by Stebbing (1888 – as *Thamneus platyrrhynchus*) from off Cape Howe (38°07'S 149°18'E).

LYCAEIDAE

Lycaea Dana, 1852

Remarks. This genus is in considerable taxonomic confusion and a thorough revision is needed to enable accurate specific determination. Harbison & Madin (1976) discuss some of the taxonomic difficulties and provide a provisional key to eight species. Of these, Vinogradov *et al.* (1982) recognise only three, but they regard one species, considered synonymous with *L. pulex* Marion, 1874 by Harbison & Madin (1976), as valid and include *Pseudolycaea pachypoda* Claus, 1879 and a new species described by Volkov.

Lycaea vincentii Stebbing

Lycaea vincentii Stebbing, 1888: 1563-1566, pl.199.

Material examined. 1 male (6.0 mm), 1 female (2.4 mm) from stations JP 71-8 (AM P39859 - 1 m) and JP 89-2 (AM P39860 - 1 f).

Diagnosis. Gnathopods 1 and 2, article 5 rectangular with sharp posterodistal projection; article 6, posterodistal corner produced below base of dactyl; articles 5 and 6 with small serrations on posterior and distal margins. Pereopods 3-6, dactyls relatively short, those of pereopods 3 and 4 one fifth to two fifths length article 6. Pereopod 7, article 2 length about 3 times articles 3-7 combined. Uropods 1 and 2, endopod not fused with peduncle. Uropod 1, exopod length slightly less than one third peduncle.

Remarks. In the past this species, like so many others, has been considered a synonym of *L. pulex*. However, Harbison (1976) and Harbison & Madin (1976) consider it a valid species. The present specimens are in agreement with the findings of these authors and with Stebbing's original description. They differ only in that article 6 of pereopod 5 has smooth margins as in *L. bovallioides* Stephensen, 1925 but the dactyl is very short, typical of *L. vincentii*.

Distribution. Common in tropical regions. Previous records from Australian waters are by Young & Anderson (1987) and Zeidler (1978).

OXYCEPHALIDAE

Calamorhynchus Streets, 1878

Remarks. This genus has been revised by Fage (1960) and is considered to be monotypic.

Calamorhynchus pellucidus Streets

Calamorhynchus pellucidus Streets, 1878: 285-286, pl.2 fig.5.
Calamorhynchus rigidus Stebbing, 1888: 1600-1602, pl.206.

Material examined. 1 female (15.0 mm) from station JP 71-2 (AM P39861).

Diagnosis. Head longer than pereon, produced into pointed rostrum, expanded into broad, lateral flanges. Gnathopods 1 and 2 chelate, articles 5 and 6 with serrations on posterior and distal margin. Pereopod 7 complete; article 2 slightly longer than articles 3-7 combined. Double urosomite more than 3 times as long as wide. Uropods with normal rami. Uropod 3 shorter than telson; endopod fused with peduncle.

Remarks. This species is easily recognised by the rostrum which is expanded into broad lateral flanges, a feature not found in any other species of Oxycephalidae.

Distribution. Although uncommon it is widely distributed in tropical and temperate regions. It was first recorded from Australian waters by Young & Anderson (1987).

Oxycephalus Milne Edwards, 1830

Remarks. This genus has been revised by Fage (1960), who recognised three species. To this should be added *P. longipes* Spandl, 1927. All four species were represented in the present collection. Vinogradov *et al.* (1982) provide the only satisfactory key to species.

Oxycephalus clausi Bovallius

?*Oxycephalus tuberculatus* Bate, 1862: 343, pl.54 fig.5.
Oxycephalus clausi Bovallius, 1887: 35-36.
Oxycephalus erythraeus Cecchini, 1929: 482-483, pl.2.
Oxycephalus mancinii Cecchini, 1929: 483-484, pl.3.

Material examined. 52 females (12.8-32.4 mm), 39 males (9.0-25.2 mm) from stations JP 71-2 (AM P39862 - 9 f, 10 m); JP 71-3 (AM P39863 - 14 f, 5 m; SAM C4222 - 5 f, 5 m); JP 71-4 (AM P39864 - 1 m); JP 71-7 (AM P39865 - 2 f); JP 71-8 (AM P39866 - 5 f, 9 m) and JP 72-23 (AM P39867 - 17 f, 9 m).

Diagnosis. Head a little longer than first 5 pereonites. Epimeral plates with sharp, medial spine on distal margin in addition to posterodistal corner. Gnathopods 1 and 2, article 5, anterodistal corner produced into sharp point, above article 6; carpal process and posterior margin of article 6 with irregular serrations. Pereopod 7, article 2 subovate, about as wide a long; distinctly longer than articles 3-7 combined. Double urosomite only slightly longer than wide. Telson slightly longer than uropod 3.

Remarks. *Oxycephalus clausi* is most readily distinguished from its congeners by the shape of the gnathopods and by the medial spine on the distal margin of the epimeral plates (in addition to posterodistal corner).

Two ovigerous females were captured in August (JP 72-23).

Distribution. A relatively common species widely distributed in tropical and temperate regions. Previous records from Australian waters are by Barnard (1931), Dakin & Colefax (1940), Sheard (1965), Young & Anderson (1987) and Zeidler (1978).

Oxycephalus latirostris Claus

Oxycephalus latirostris Claus, 1879b: 47.
Oxycephalus pectinatus Bovallius, 1887: 36.
Oxycephalus notabilis Spandl, 1924: 32.

Material examined. 1 male (16.5 mm) from station JP 71-8 (AM P39868).

Diagnosis. Head slightly shorter than pereon. Gnathopods 1 and 2, carpal process and article 6, cutting edges with separate row of closely packed, sharp spines. Pereopod 7, article 2 rhomboid, about as wide as long, slightly shorter than articles 3-7 combined. Double urosomite, width about three fifths length. Telson slightly longer than uropod 3.

Remarks. A distinctive feature of this species is the finely serrate ornamentation of the cutting edges of the chela (articles 5 and 6 of gnathopods 1 and 2) (see Pillai, 1966: 178).

Distribution. An uncommon species recorded mainly from tropical regions. It was first recorded from Australian waters by Young & Anderson (1987).

Oxycephalus longipes Spandl

Fig.22

Oxycephalus longipes Spandl, 1927: 181-182, fig.14.

Material examined. 1 ovigerous female (approximately 23 mm - rostrum damaged) from station JP 71-3 (AM P39869).

Diagnosis. Head about as long as pereon. Gnathopod 1, carpal process and article 6, cutting edges with series of sharp serrations. Gnathopod 2, cutting edges of chela with series of compact, rounded teeth. Pereopod 7, article 2 gradually narrowed distally, about twice as long as wide, as long as articles 3-7 combined; article 6 styliform, slightly longer than articles 3-5 combined. Double urosomite, width about three fifths length. Telson slightly shorter than uropod 3.

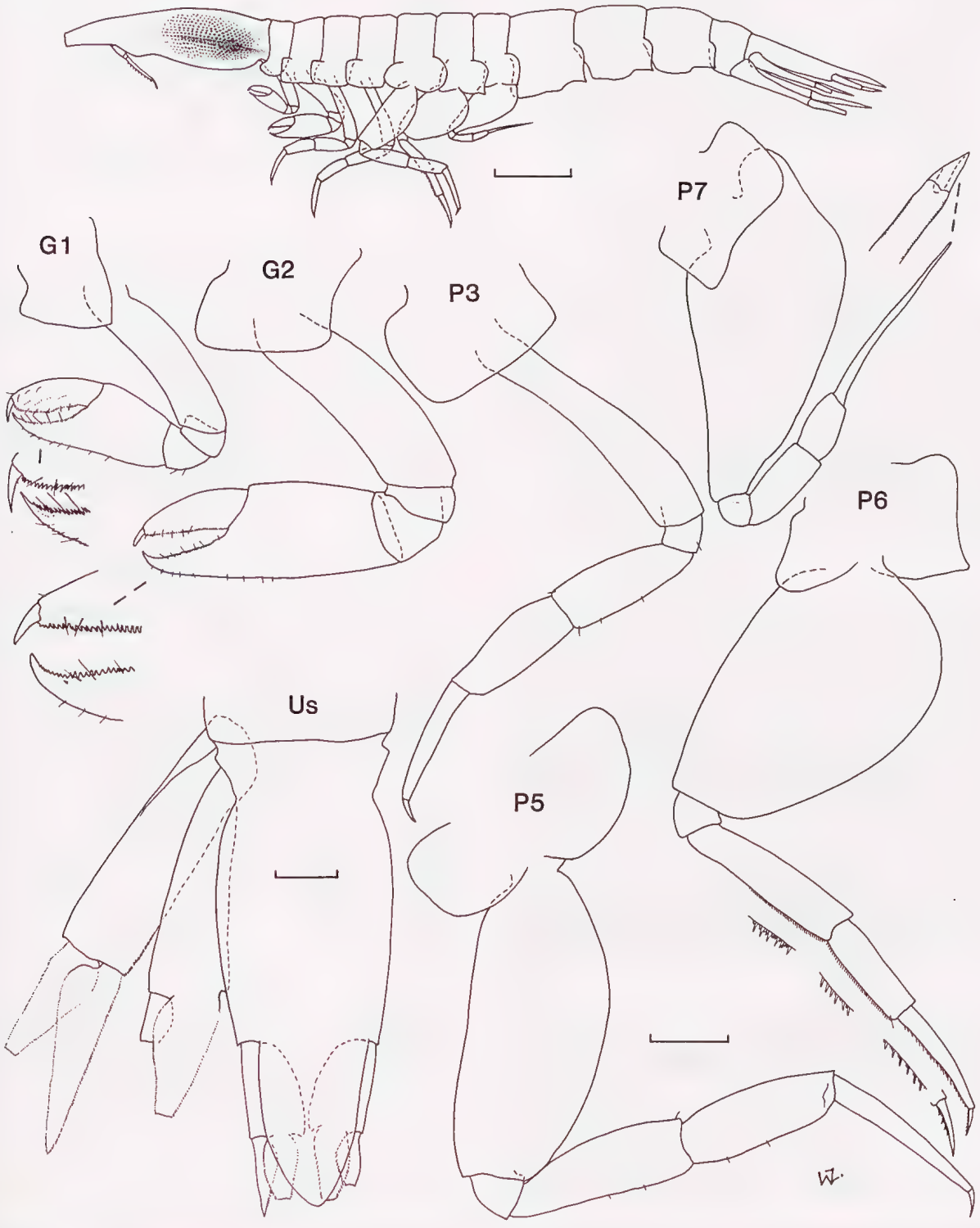

Fig.22. *Oxycephalus longipes* Spandl, female approximately 23.0 mm (scales = 2.0 mm, 0.5 mm).

Remarks. The present specimen is in perfect agreement with the figures and description given for this species by Spandl (1927). It has not been recorded in the literature since its original description and Fage (1960) makes no mention of it in his list of Oxycephalidae and proposed synonymies. It is possible that if collected in the past it may have been confused with other species of *Oxycephalus*, however, apart from the shape and ornamentation of the gnathopods, this species is readily distinguished by the extremely long, slender article 6 of pereopod 7.

Distribution. Spandl recorded it (one female) from the tropical Atlantic (5°27'N 21°41'W). It is a new record for Australian waters and the southern hemisphere.

Oxycephalus piscator Milne Edwards

Oxycephalus piscatoris Milne-Edwards 1830: 396.
Orio ornithorhamphus Cocco, 1832: 205.
Oxycephalus oceanicus Guérin-Méneville, 1836: 10, pl.18 fig.2.
Oxycephalus piscator Milne-Edwards, 1840: 100-101, pl.30 fig.10.
Ornithorhamphus coccoi Natale, 1850: 12, pl.1 fig.3.
Natalius candidissimus Costa, 1864: 88.
Oxycephalus bulbosus Streets, 1878: 280-281, pl.2 fig.2.
Oxycephalus similis Claus, 1879b: 47.
Oxycephalus edwardsii Thomson, 1883: 238, pl.12 figs 14-21.

Material examined. 1 male (14.2 mm) from station JP 71-3 (AM P39870).

Diagnosis. Head slightly shorter than pereon. Gnathopods 1 and 2, carpal process and posterior margin of article 6 with irregular serrations. Pereopod 7, article 2 rhomboid, slightly longer than wide; about as long as articles 3-7 combined. Double urosomite, width about three fifths length or slightly more. Telson slightly shorter than uropod 3.

Remarks. This species is very similar to *O. clausi* but is easily distinguished by the shape of the gnathopods and the lack of a medial spine on the distal margin of the epimeral plates.

Distribution. An uncommon but widely distributed species known mainly from tropical regions. It was first recorded from Australian waters by Young & Anderson (1987).

Rhabdosoma White, 1847

Remarks. Species of this genus are distinguished by the extremely slender, elongate body and the very long, needle-shaped rostrum. The genus has been revised by Fage (1960), who recognised four species and provides a key (in French), together with useful illustrations.

Rhabdosoma brevicaudatum Stebbing

Fig.23

Rhabdosoma brevicaudatum Stebbing, 1888: 1612-1615, pl.208.
Xiphocephalus brevicaudatus.–Bovallius, 1890: 118.
Rhabdosoma brachyteles Stebbing, 1895: 369-370, pl.55B.
Pseudanurus brevicaudatus.–Garbowski, 1895: 199.

Material examined. 2 females (approximately 24 mm - damaged) from station JP 72-23 (AM P39871).

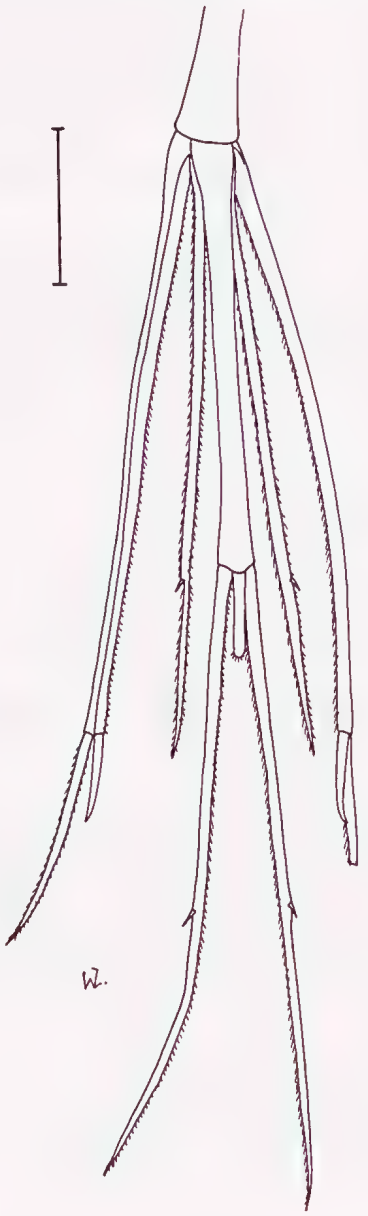

Fig.23. *Rhabdosoma brevicaudatum* Stebbing, uropoda and telson from female approximately 24.0 mm (scale = 1.0 mm).

Diagnosis. Both sexes with gills on pereonites 5 and 6. Gnathopods 1 and 2, carpal process sharp, extending just beyond article 6; article 6, posterodistal corner, rounded, slightly produced. Uropods 2 and 3, exopod rudimentary, length much less than half endopod. Telson rounded terminally, length much less than one quarter last urosomite, not reaching limit of uropod 2.

Remarks. This species is most similar to *R. minor* Fage, 1954 which also has a short telson. However, in *R. minor* the telson is relatively longer, equal in length to half the last urosomite and reaching the limit of uropod 2. One of the females is ovigerous.

Distribution. A relatively uncommon species recorded mainly from tropical regions. It is a new record for Australian waters.

Rhabdosoma whitei Bate

Rhabdosoma whitei Bate, 1862: 345-346, pl.54 fig.7.
Rhabdosoma investigatoris Giles, 1887: 219, pl.4.
Xiphocephalus lilljeborgi Bovallius, 1890: 118, pl.7 figs 1-20.
Rhabdosoma piratum Stebbing, 1895: 368-369, pl.55A.

Material examined. 3 females (48.2-57.0 mm), 2 males (damaged) from stations JP 71-3 (AM P39872 - 1 m); JP 71-8 (AM P39873 - 1 f) and JP 72-23 (AM P39874 - 2 f, 1 m).

Diagnosis. Females with gills on pereonites 2-6; males with gills on pereonites 5 and 6. Gnathopods 1 and 2, carpal process sharp, extending just beyond article 6; article 6, posterodistal corner rounded, slightly produced in females; that of gnathopod 1, of males, produced to middle of dactyl. Uropods 2 and 3, exopod well developed, length about two thirds endopod. Telson sharp terminally, length much longer than last urosomite, slightly longer than uropod 3.

Remarks. This species is similar to *R. armatum* (Milne-Edwards, 1840) but is easily distinguished from that species by the lack of an additional tooth-like process on the carpal process of gnathopod 1 and by the relatively well-developed exopods of uropods 2 and 3.

Distribution. A relatively common, widespread species, recorded mainly from tropical and subtropical regions. Previous records from Australian waters are by Barnard (1931), Dakin & Colefax (1940 – as *R. lilljeborgi*), Sheard (1965), Young & Anderson (1987) and Zeidler (1978).

Streetsia Stebbing, 1888

Remarks. This genus has been revised by Fage (1960) who recognised four species and provides a key (in French) together with useful illustrations. Pillai (1966) also provides a key together with illustrations of each species.

Streetsia challengeri Stebbing

?*Oxycephalus pronoides* Bovallius, 1887: 37.
Streetsia challengeri Stebbing, 1888: 1603-1606, pl.207.
Streetsia stebbingi Chevreux, 1900: 161, pl.18 fig.4.
Streetsia washingtoni Senna, 1902: 15, pl.2.
Streetsia sabauda Colosi, 1918: 218, pl.17 figs 5-9.
Streetsia gaussi Spandl, 1927: 184, fig.17.

Material examined. 32 females (8.4-42.8 mm), 10 males (11.6-33.1 mm) from stations JP 71-3 (AM P39875 - 9 f, 1 m); JP 71-4 (AM P39876 - 6 f, 2 m; SAM C4223 - 3 f, 1 m); JP 71-7 (AM P39877 - 6 f); JP 71-8 (AM P39878 - 7 f, 3 m) and JP 72-23 (AM P39879 - 1 f, 3 m).

Diagnosis. Body relatively slender. Head about as long as pereon and pleon. Gnathopod 1, article 5 about as wide as long, carpal process roughly serrated on distal and posterodistal margin, apical tooth slightly longer than others with distal orientation. Gnathopod 2, article 2, posterodistal corner expanded into triangular lobe in mature females; carpal process with sharp tooth produced beyond dactyl. Double urosomite, length almost twice width, distinctly shorter than telson.

Remarks. The present specimens have a cuticular pore on the epimeral plates similar to that found in *S. mindanaonis* (Stebbing, 1888). However, *S. challengeri* is easily distinguished from *S. mindanaonis* by the shape of the gnathopods and in mature females the posterodistal corner of article 2 of gnathopod 2 is expanded into a triangular lobe, a feature not found in any other species of *Streetsia*.

Thirteen ovigerous females were captured in March (JP 71-3, 71-4, 71-7, 71-8).

Distribution. A very common, widely distributed species recorded mainly from tropical regions. Previous records from Australian waters are by Guiler (1952), Sheard (1965) and Young & Anderson (1987).

Streetsia porcella (Claus)

?*Orio oxyahingus* Prestandrea, 1833: 10.
Oxycephalus porcellus Claus, 1879b: 48.
Streetsia intermedia Spandl, 1927: 188-190, figs 20,21.
Streetsia nyctiphanes Fage, 1934: 1631.

Material examined. 1 ovigerous female (16.0 mm) from station JP 71-3 (AM P39880).

Diagnosis. Body robust. Head as long or a little longer than pereon. Gnathopod 1, article 5 about as wide as long, carpal process roughly serrated on distal and posterodistal margin, apical tooth slightly longer than others with distal orientation. Gnathopod 2, article 5 quadrate, carpal process with sharp tooth produced beyond dactyl. Double urosomite slightly longer than wide, about three quarters length telson.

Remarks. This species is most similar to *S. challengeri* but is readily distinguished by the general body shape, the form of gnathopod 2 and by the relatively shorter double urosomite.

Distribution. An uncommon but widely distributed species recorded mainly from tropical regions. It was first recorded from Australian waters by Young & Anderson (1987).

Streetsia steenstrupi (Bovallius)

?*Oxycephalus longiceps* Claus, 1879b: 48.
Oxycephalus steenstrupi Bovallius, 1887: 37.

Material examined. 1 female, 1 male (approximately 12 mm - damaged) from station JP 71-8 (AM P39881).

Diagnosis. Body relatively slender. Head almost as long as pereon and pleon. Gnathopod 1, article 5 distinctly longer than wide, carpal process with relatively smooth margins covered in long setae, apical tooth orientated about 45° posteriorly to distal margin; article 6 with posterodistal corner produced partly overlapping dactyl. Gnathopod 2, carpal process with large tooth produced just beyond dactyl. Double urosomite, length almost twice width, slightly longer than telson.

Remarks. This species is most readily distinguished from all its congeners by the shape of gnathopod 1.

Distribution. A relatively rare species recorded mainly from tropical regions. Previous records from Australian waters are by Young & Anderson (1987) and Zeidler (1978).

Platyscelidae

Hemityphis Claus, 1879

Remarks. This genus is currently considered to be monotypic (Harbison *et al.*, 1977).

Hemityphis rapax (Milne Edwards)

Typhis rapax Milne Edwards 1830: 395.
Thyropus rapax.–Bate, 1862: 329.
Hemityphis tenuimanus Claus 1879b: 12-13.
Schizoscelus rapax.–Bovallius, 1887: 44.

Material examined. 2 females (5.7 and 5.8 mm), 1 male (7.0 mm) from stations JP 71-7 (AM P39882 - 1 m) JP 71-8 (AM P39883 - 1 f) and JP 72-23 (AM P39884 - 1 f).

Diagnosis. Antenna 2 of male, 2 distal articles longer than half preceding article. Gnathopod 1, carpal process with slightly serrated margins, extending to about half article 6; article 6, posterior margin with very fine serrations, almost smooth. Gnathopod 2, carpal process with slightly serrate margins, extending to about three quarters article 6; article 6, posterior margin with fine serrations. Pereopod 6, article 2 with small, curved fissure.

Remarks. This species is distinguished by the form of the gnathopods and pereopod 6 and is separated from the closely related genus *Platyscelus* on the basis of the second antennae of males in which the last two segments are more than half the length of the preceding segment. In *Platyscelus* these segments are much less than half the length of the preceding segment.

One ovigerous female (5.8 mm) was captured in March (JP 71-8).

Distribution. Widespread in tropical and warm temperate regions. The only previous record from Australian waters is by Stebbing (1888 – as *H. tenuimanus*).

Paratyphis Claus, 1879

Remarks. Species of *Paratyphis* are difficult to identify with certainty and the genus is in need of revision. Vinogradov *et al.* (1982) recognise four species and provide useful illustrations and a key (in Russian). Pirlot (1930) also provides a key to species (in French).

Paratyphis parvus Claus

Paratyphis parvus Claus, 1887: 40, pl.7 figs 13-21.
Paratyphis pacificus Stebbing, 1888: 1479-1480.

Material examined. 1 male (3.6 mm) from station JP 72-23 (AM P39885).

Diagnosis. Antenna 2 of male, 2 distal articles slightly longer than half preceding article. Gnathopod 1, article 5 with angular anterodistal and posterodistal corners (not rounded). Gnathopod 2, carpal process pointed with serrated margins, extending to about one third article 6. Pereopod 5, article 2 with notch on distal margin for insertion of following articles. Pereopod 6, article 2 with relatively small, crescent-shaped fissure.

Remarks. The best distinguishing character of *P. parvus* appears to be the form of the gnathopods. It is most similar to *P. maculatus* Claus, 1879 but in that species the carpal process of gnathopod 2 is very short and has smooth margins.

Distribution. A relatively rare species recorded from tropical and warm temperate regions. Previous records from Australian waters are by Young & Anderson (1987) and Zeidler (1978).

Platyscelus Bate, 1862

Remarks. This genus is in need of revision. Vinogradov *et al.* (1982) recognise four species and provide a key (in Russian) together with useful illustrations.

Platyscelus armatus (Claus)

Figs 24, 25

?*Dithyrus faba* Dana, 1852: 1010, pl.69 fig.3.
?*Platyscelus rissoinae* Bate, 1862: 329-330, pl.52 fig.9.
Eutyphis armatus Claus, 1879b: 10-11.
Eutyphis inermis Claus, 1887: 37.
?*Eutyphis forfex* Bovallius, 1887: 46.
Platyscelus armatus var. *inermis*.–Shoemaker, 1945: 255, fig.46.

Material examined. 2 females (5.9 and 17.4 mm) from stations JP 71-3 (AM P39886) and JP 71-7 (AM P39887).

Diagnosis. Epimeral plates with midlateral ridge folding against article 2 of pereopod 6. Gnathopod 1, carpal process with serrated margins almost as long as article 6; article 6, posterior margin serrated; articles 3-5 with long setae. Gnathopod 2 like gnathopod 1 but carpal process extended just beyond dactyl. Pereopods 3 and 4, article 6 with posterodistal corner slightly excavate. Pereopods 5 and 6, coxal plates with lateral process, larger on fifth (absent or reduced in juveniles). Uropod 3, exopod length distinctly greater than half endopod.

Remarks. This species is usually easily distinguished from its congeners by the lateral process on the fifth and sixth coxal plates. However, sometimes smaller specimens are found without these processes and in the past these have been considered a separate species or variety of *P. armatus* (Shoemaker, 1945). In the present collection the smaller specimen (Fig.25) not only lacks the lateral projections on the coxal plates but pereopod 7 has a full compliment of articles. Additional differences from the large specimen are as follows: i) gnathopod articles 5 and 6 are more coarsely serrate and article 5 is not as produced; ii) pereopod 5, article 2 is more rounded distally with a small notch near the insertion of article 3; and iii) pereopod 6, article 2 has a small notch near the posterodistal corner and articles 4 and 5 are more coarsely serrate. These differences are probably related to maturity rather than of specific significance as the two specimens are otherwise very similar. Variations in the number of articles of pereopod 7 amongst Platyscelidae have been observed by other authors (e.g., Barnard, 1937; Spandl, 1927) and Stephensen (1925) records a juvenile *Platyscelus* with pereopod 7 complete, similar to the present specimen. The number of articles of pereopod 7 is therefore not a good character alone to separate the families Platyscelidae and Parascelidae. The best distinguishing feature is the shape of the mouthparts which form a broad rounded cylinder in Platyscelidae and a sharp, pointed cone in Parascelidae.

The large specimen, captured in March, is ovigerous.

Distribution. A relatively rare species known from widely scattered records from tropical and warm temperate regions. It is a new record for Australian waters.

Platyscelus ovoides (Risso)

Typhis ovoides Risso, 1816: 122, pl.2 fig.9.
Typhis ferus Milne-Edwards, 1830: 395, pl.11 fig.8.
Platyscelus serratus Bate, 1862: 330-332, pl.52 figs 10,11.
Platyscelus intermedius Thomson, 1879: 244.
Eutyphis ovoides.–Claus, 1879b: 9.
Eutyphis globosus Claus, 1879b: 12.

Material examined. 24 females (6.3-16.0 mm), 19 males (6.3-14.6 mm) from stations JP 71-3 (AM P39888 - 10 f, 2 m; SAM C4224 - 4 f, 3 m); JP 71-4 (AM P39889 - 2 m); JP 71-7 (AM P39890 - 1 f, 1 m); JP 77-18 (AM P39891 - 1 f); JP 77-19 (AM P39892 - 1 f, 1 m); JP 77-26 (AM P39893 - 4 f, 10 m) and JP 77-28 (AM P39894 - 3 f).

Diagnosis. Body very globular. Gnathopod 1, carpal process with serrated margins, a little shorter than article 6; article 6, posterior margin serrated, anterior margin serrated for distal third; articles 4 and 5 with few long setae. Gnathopod 2 like gnathopod 1 but carpal process extended to limit of article 6. Uropod 3, exopod length distinctly less than half endopod.

Remarks. The globular shape of the body and the form of the gnathopods distinguish this species from its congeners.

Five ovigerous females (approximately 13 mm) were captured in March (JP 71-3) and December (JP 77-26).

Distribution. A widely distributed species, recorded mainly from tropical regions. First recorded from Australian waters by Young & Anderson (1987).

Platyscelus serratulus Stebbing

Eutyphis serratus Claus, 1879b: 11-12.
Platyscelus serratulus Stebbing, 1888: 1470-1471.
Platyscelus dubius Shoemaker, 1925: 51-54, figs 20,21.

Material examined. 3 females (5.1-16.7 mm), 1 male (15.0 mm) from stations JP 71-7 (AM P39895 - 1 m); JP 72-23 (AM P39896 - 2 f) and JP 77-25 (AM P39897 - 1 f).

Diagnosis. Gnathopod 1, carpal process with serrated margins, a little shorter than article 6; article 6, posterior margin serrated; articles 3-5 with very few, long setae. Gnathopod 2 like gnathopod 1 but carpal process extended to limit of article 6. Uropod 3, exopod length distinctly greater than half endopod.

Remarks. This species is very similar to *P. ovoides* but can be distinguished from it by the gnathopods which

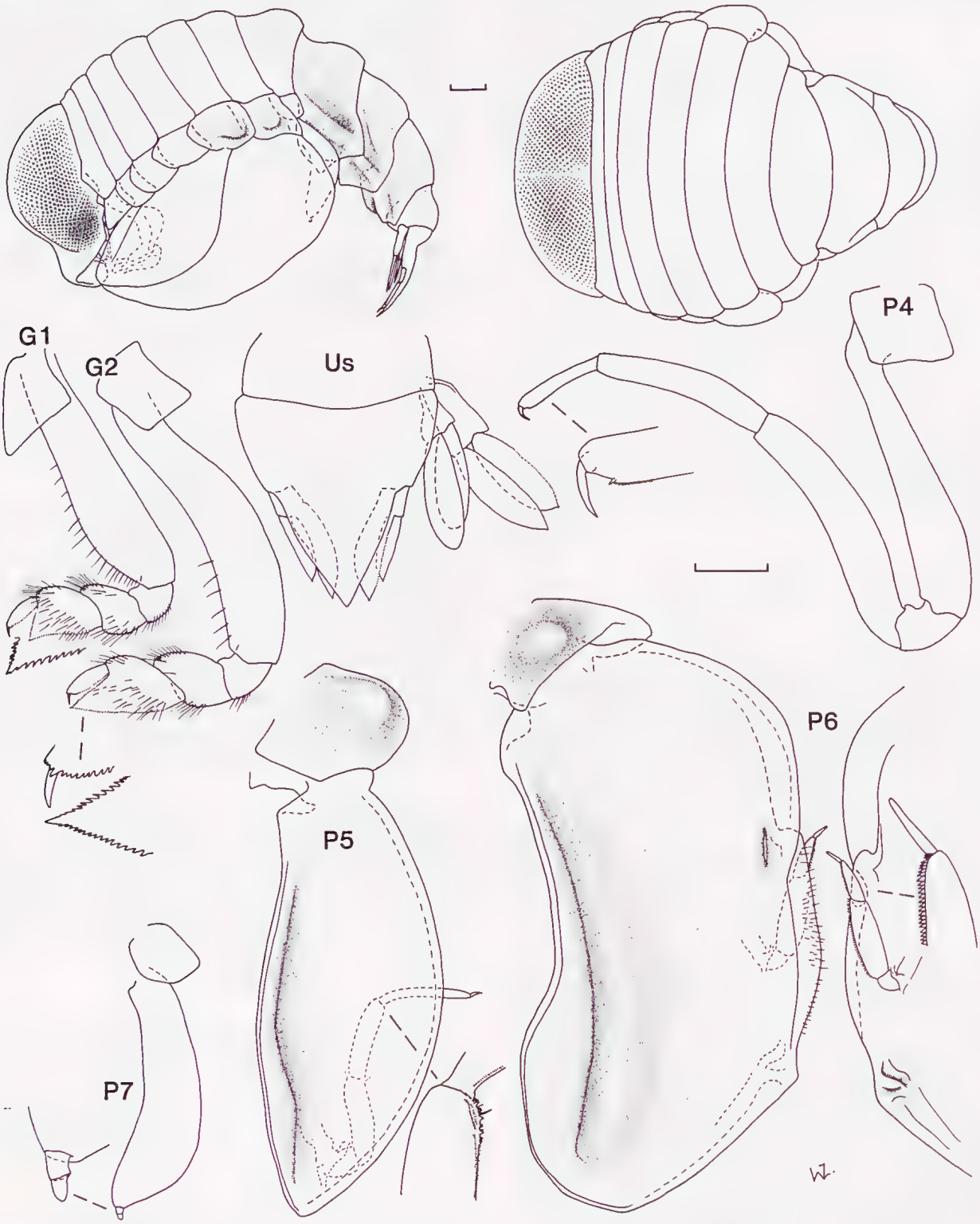

Fig.24. *Platyscelus armatus* (Claus), female 17.4 mm from station JP 71-3 (scales = 1.0 mm).

lack serrations on the anterior margin of article 6.

One ovigerous female (16.7 mm) was captured in December (JP 77-25).

Distribution. Widely distributed in tropical and subtropical regions. Previous records from Australian waters are by Watson & Chaloupka (1982), Young & Anderson (1987) and Zeidler (1978).

Tetrathyrus Claus, 1879

Remarks. Pirlot (1930) considers this genus to be monotypic and synonymises the six nominal species with *T. forcipatus* Claus, 1879 but Vinogradov *et al.* (1982) also recognise *T. arafurae* Stebbing, 1888 as a valid species based mainly on that species having uropods 2 and 3 with free endopods. However, during my studies

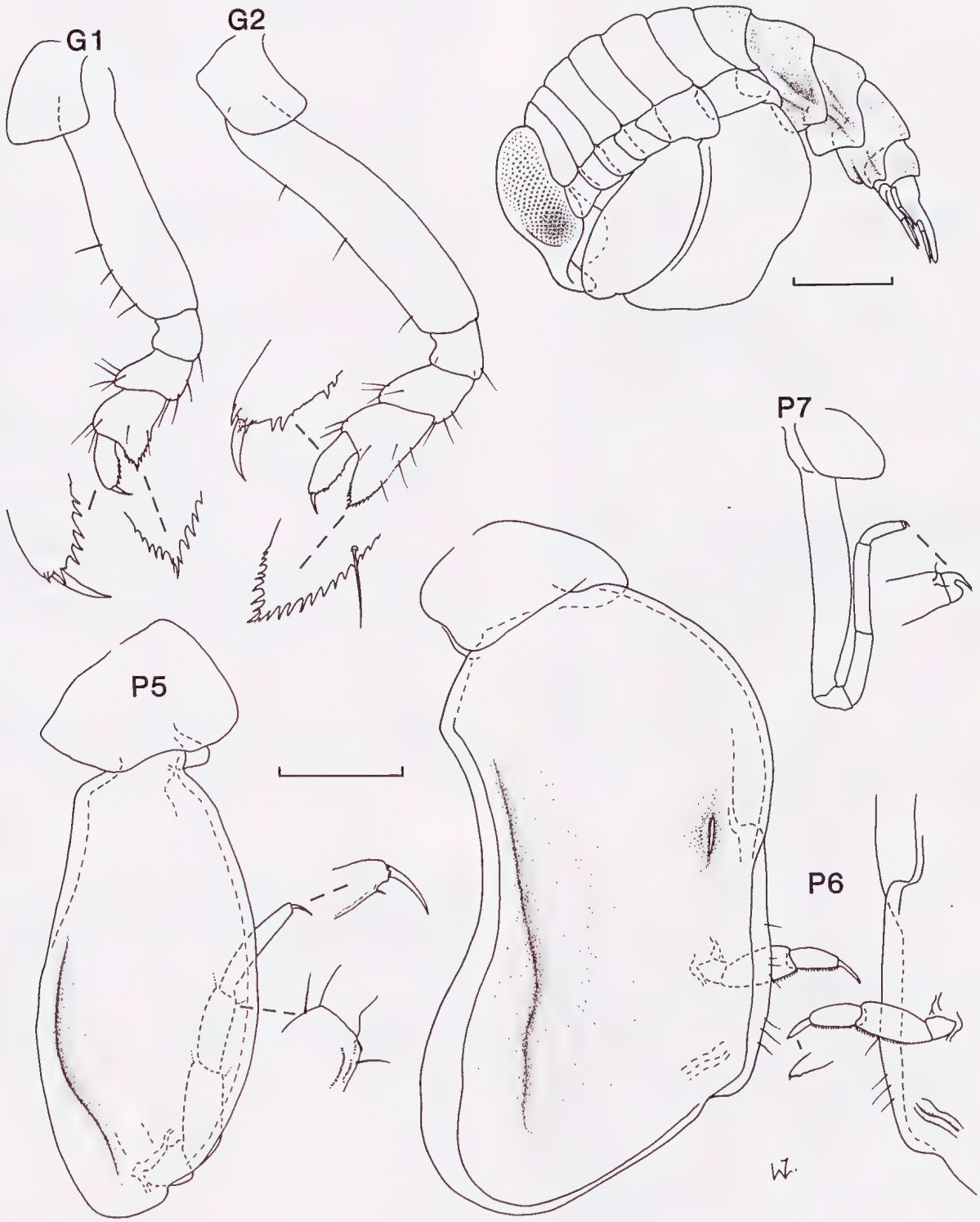

Fig.25. *Platyscelus armatus* (Claus), female 5.9 mm from station JP 71-7 (scales = 1.0 mm, 0.5 mm).

of *T. forcipatus* (Zeidler, 1978), I found the fusion of the endopod with the peduncle of uropod 2 to be variable and thus an unreliable character, although I never found a specimen in which the endopod of uropod 3 was free. The genus is thus in need of further revision in order to determine the number of valid species present.

Tetrathyrus forcipatus Claus

Tetrathyrus forcipatus Claus, 1879b: 14-15.
Tetrathyrus rectangularis Bovallius, 1887: 47.
Tetrathyrus inscriptus Bovallius, 1887: 48.
Tetrathyrus moncoeuri Stebbing, 1888: 1480-1483, pl.184.
Tetrathyrus sancti-josephi Shoemaker, 1925: 54, figs 22-24.

Material examined. 1 female (3.0 mm) from station JP 89-3 (AM P39898).

Diagnosis. Antenna 2 of male, 2 distal articles longer than half preceding article. Gnathopods 1 and 2, dactyl closing against concave distal margin of article 6. Pereopod 6, article 2 without fissure. Endopod of uropod 2 (usually) and uropod 3, fused with peduncle. Telson, length subequal to, or slightly shorter than, double urosomite.

Remarks. According to Vinogradov *et al.* (1982) *T. arafurae* can be distinguished from *T. forcipatus* by the following characters: i) pereopod 5, article 2 is distinctly more than twice as long as wide; ii) uropods 2 and 3, endopods are not fused with peduncle; and iii) the telson is distinctly longer than double urosomite.

Distribution. Relatively abundant in subtropical waters of the world's oceans. Previous records from Australian waters are by Barnard (1931), Dakin & Colefax (1940 – as *T. moncoeuri*), Stebbing (1888 – as *T. moncoeuri*) and Zeidler (1978).

Parascelidae

Parascelus Claus, 1879

Remarks. Bowman & Gruner (1973) regard *Parascelus* a junior synonym of *Thyropus*. However, Vinogradov *et al.* (1982) make a case for removing *Parascelus* from the synonymy of *Thyropus*; *Parascelus* comprising those species in which article 2 of pereopod 6 is without a fissure. Until a much needed revision of the family is undertaken I have decided to recognise both genera. Harbison *et al.* (1977) provide a provisional key to the species of both genera (five species, all as *Thyropus*) but include *Parascelus parvus* Claus, 1879 which Vinogradov *et al.* (1982) regard as a synonym of *P. edwardsi* Claus, 1879.

Parascelus typhoides Claus

Parascelus typhoides Claus, 1879b: 19-20.

Material examined. 2 females (3.8 and 4.8 mm) from station JP 72-23 (AM P39899).

Diagnosis. Gnathopod 1 distinctly shorter than gnathopod 2. Gnathopod 1, article 2 longer than articles 3-7 combined; article 5, posterodistal and anterodistal corners produced into very short, rounded lobes. Pereopod 6, article 2 without fissure, only slightly narrowed for distal half; article 4, anterodistal corner produced, partly overlapping article 5. Uropods 2 and 3, exopod length slightly less than half endopod.

Remarks. *Parascelus typhoides* is very similar to *P. edwardsi*, the only other congener recognised by Vinogradov *et al.* (1982). The main difference appears to be in the shape of the basis of pereopod 6 which in *P. edwardsi* is distinctly narrowed for the distal half. In the present specimens the gnathopods and pereopod 6 tend to agree with available descriptions and figures of *P. typhoides* but the uropods are more like *P. edwardsi*.

The specimen described as *P. typhoides* by Zeidler (1978) has been re-examined and appears to resemble *P. edwardsi* more so than *P. typhoides*.

Regarding *P. similis* Stephensen, 1925, Vinogradov *et al.* (1982) consider it a synonym of *P. typhoides*. However, I believe that it is a species of *Thyropus* as Stephensen clearly describes and illustrates a fissure on the basis of pereopod 6, similar to that found in *T. sphaeroma* (Claus, 1879), but which is absent in both species of *Parascelus*.

Distribution. A relatively rare species, widely distributed in tropical and temperate regions. The only previous record from Australian waters (Zeidler, 1978) may be a misidentification of *P. edwardsi*.

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Mrs D. Lowery typed the manuscript.

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APPENDIX I

Station Collection Data

JP 71-2 Tasman Sea, 75 km east of Port Hacking, NSW (34°09'S 152°07'E - 34°20'S 152°05'E), 0-550 m in water of depth 2470-3110 m, 23 Mar. 1971, M. Gregory & J. Paxton (3 m Isaacs-Kidd midwater trawl).

JP 71-3 Tasman Sea, 75 km east of Port Hacking, NSW (34°10'S 151°59'E - 34°09'S 152°05'E), 0-60 m in water of depth 1810-2470 m, 24 Mar. 1971, M. Gregory & J. Paxton (3 m Isaacs-Kidd midwater trawl).

JP 71-4 Tasman Sea, 95 km east of Port Hacking, NSW (34°09'S 152°07'E - 34°14'S 152°14'E), 0-250 m in water of depth 2470-2560 m, 24-25 Mar. 1971, M. Gregory & J. Paxton (3 m Isaacs-Kidd midwater trawl).

JP 71-7 Tasman Sea, 95 km east of Port Hacking, NSW (34°10'S 152°16'E - 34°00'S 152°14'E), 0-350 m in water of depth 2743-2835 m, 25 Mar. 1971, M. Gregory & J. Paxton (3 m Isaacs-Kidd midwater trawl).

JP 71-8 Tasman Sea, 95 km east of Port Hacking, NSW (34°03'S 152°12'E - 34°14'S 152°14'E), approximately 600 m in water of depth 2380-2835 m, 25-26 Mar. 1971, M. Gregory & J. Paxton (3 m Isaacs-Kidd midwater trawl).

JP 72-23 Tasman Sea, 30 km east of Port Jackson, NSW (33°52'S 151°37'E), 18-55 m in water of depth 146 m, 10 Aug. 1972, J. Paxton & D. Griffin (3 m Isaacs-Kidd midwater trawl).

K 72-07-01 Tasman Sea, 45 km east of Port Hacking, NSW (34°00'S 151°43'E), 503 m, 6 Nov. 1972 (otter trawl).

K 73-01-11 Tasman Sea, east of Port Jackson, NSW, 73-110 m in water of depth 183-220, 2 July 1973, K. Graham (midwater trawl).

K 74-05-01 Tasman Sea, 50 km east of Port Kembla, NSW (34°28'S 151°29'E), 0-230 m in water of depth 1417 m, 22 July 1974, J. Paxton & K. Graham (midwater trawl).

JP 77-17 Tasman Sea, 90 km east of Broken Bay, NSW (33°33'S 152°18'E), 0-140 m in water of depth 2012 m, 12 Dec. 1977, D. Blake, H. Larson, A. Reynolds & J. Paxton (15 x 20 m Engel midwater trawl).

JP 77-18 Tasman Sea, 95 km east of Broken Bay, NSW (33°31'S 152°20'E), 0-900 m in water of depth 1830-2926 m, 12-13 Dec. 1977, J. Paxton *et al.* (15 x 20 m Engel midwater trawl).

JP 77-19 Tasman Sea, 100 km east of Broken Bay, NSW (33°29'S 152°25'E), 0-900 m in water of depth 1830-2743 m, 13 Dec. 1977, J. Paxton *et al.* (15 x 20 m Engel midwater trawl).

JP 77-22 Tasman Sea, 105 km east of Tuggerah Lake, NSW (33°23'S 152°37'E), 0-625 m in water of depth 2926 m, 13 Dec. 1977, J. Paxton *et al.* (15 x 20 m Engel midwater trawl).

JP 77-25 Tasman Sea, 95 km east of Tuggerah Lake, NSW (33°20'S 152°32'E), 0-350 m in water of depth 2377 m, 14 Dec. 1977, J. Paxton *et al.* (15 x 20 m Engel midwater trawl).

JP 77-26 Tasman Sea, 110 km east of Broken Bay, NSW (33°28'S 152°33'E), 0-1000 m in water of depth 4206 m, 14 Dec. 1977, J. Paxton *et al.* (15 x 20 m Engel midwater trawl).

JP 77-27 Tasman Sea, 74 km east of Port Jackson, NSW (33°53'S 152°02'E), 0-800 m in water of depth 1830 m, 14 Dec. 1977, J. Paxton *et al.* (15 x 20 m Engel midwater trawl).

JP 77-28 Tasman Sea, 93 km east of Wollongong, NSW (34°20'S 151°56'E), 0-800 m in water of depth 2926-3658 m, 14-15 Dec. 1977, J. Paxton *et al.* (15 x 20 m Engel midwater trawl).

JP 89-2 Tasman Sea, 90 km east of Port Jackson, NSW (33°50.9'S 152°15.9'E - 33°52.5'S 152°39.0'E), 0-1200 m, HMAS Cook, 28 Apr. 1989, J. Paxton *et al.*

JP 89-3 Tasman Sea, 125 km east of Port Jackson, NSW (33°52.5'S 152°39.0'E - 33°53.9'S 152°5.9'E), 0-1800 m, HMAS Cook, 27 Apr. 1989, J. Paxton *et al.*

JP 89-7 Tasman Sea, 100 km east of Cape Banks, NSW (33°58.9'S 152°19.3'E - 34°05.7'S 152°55.9'E), 0-3300 m, HMAS Cook, 29 Apr. 1989, J. Paxton *et al.*

F 19 Lord Howe Rise, Tasman Sea (29°24.57'S 160°08.73'E), epibenthic sled at 2000 m, R.V. Franklin Cruise 05/89, 4 May 1989, J.K. Lowry *et al.*

F 25 Lord Howe Rise, Tasman Sea (28°05.76'S 163°06.04'E), beam trawl at 1051 m, R.V. Franklin Cruise, 05/89, 5 May 1989, J.K. Lowry *et al.*

F 33 Lord Howe Rise, Tasman Sea (27°13.34'S 160°43.41'E), epibenthic sled at 1989 m, R.V. Franklin Cruise 05/89, 7 May 1989, J.K. Lowry *et al.*

F 34 Lord Howe Rise, east of Gifford Guyot, Tasman Sea (26°51.66'S 159°49.07'E), epibenthic sled at 2500 m, R.V. Franklin Cruise 05/89, 7 May 1989, J.K. Lowry *et al.*

F 43 Between Gifford Guyot & Britannia seamount, Tasman Sea (27°13.44'S 157°58.11'E), epibenthic sled at 2900 m, R.V. Franklin Cruise 05/89, 9 May 1989, J.K. Lowry *et al.*

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Revision of the Genus *Holonuncia* Forster (Arachnida: Opiliones: Triaenonychidae) with Description of Cavernicolous and Epigean Species from Eastern Australia

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ABSTRACT. The genus *Holonuncia* Forster and the type species *H. cavernicola* Forster are redescribed. One new combination is established: *H. seriata* (*Nuncia*) (Roewer, 1915). *Holonuncia seriata* and *H. tuberculata* (Roewer, 1915) are redescribed and ten new species described: *H. sussa, H. dewae, H. francesae, H. katoomba, H. weejasperensis, H. dispar, H. recta, H. hamiltonsmithi, H. kaputarensis* and *H. enigma*. Allozyme electrophoresis resolves some species boundary problems. Morphological adaptations to cave life include leg attenuation, depigmentation and eye regression but not loss. The distribution of the genus in eastern mainland Australian caves is illustrated.

HUNT, G.S., 1992. Revision of the genus *Holonuncia* Forster (Arachnida: Opiliones: Triaenonychidae) with description of new cavernicolous and epigean species from eastern Australia. Records of the Australian Museum 44(2): 135–163.

Species of *Holonuncia* Forster are the most widely distributed cavernicolous harvestmen in eastern mainland Australia (Fig.1). Apart from notes on cavernicolous adaptations (Hunt, 1972), no work has been done on the group since Forster (1955) described the type species from Jenolan Caves. Surface species in the genus occur across virtually the entire range of the genus, unlike the situation with the largely cavernicolous Tasmanian genus *Hickmanoxyomma* in which the single known surface species is confined to a small part of the generic range (Hunt, 1990).

Materials and Methods

Type material of all nominal species has been examined and reassessed. The following abbreviations are used to indicate the present location of material examined:

AM – Australian Museum, Sydney (usually denoted by the registration number prefix KS); ANIC – Australian National Insect Collection, CSIRO, Canberra; FIS – Forschungsinstitut Senckenberg, Frankfurt am Main; SAM – South Australian Museum,

Adelaide.

Official numbers for caves (e.g., J31) follow Matthews (1985). Terminology and methods of measurement follow Hunt (1990) except that lateral plate becomes dorsolateral plate in conformity with Martens (1986). Tergal areas are abbreviated to TA1, etc.; coxa of leg I is coxa I, etc.

Other abbreviations are: SL – scute length, CW – carapace width, PFL – pedipalp femur length, AI and AIV – astragalus I and IV lengths, CI and CIV – calcaneus I and IV lengths, MI – metatarsus I length, FIV – femur IV length, CSL – cheliceral second segment length. In general CW is used as an indication of body size as it is less subject to variation due to physiological state. Methods for allozyme electrophoresis are given at the end of the paper. Tables referred to throughout the text are listed in the Appendix.

Triaenonychidae Soerensen

Triaenonychinae Soerensen

Remarks. *Holonuncia* belongs to an assemblage of eastern Australian genera which includes *Equitius, Paranuncia, Odontonuncia, Hickmanoxyomma* and at least three undescribed genera. Their male genitalia are of the basic form that Martens (1986) ascribes to Australian and New Zealand Triaenonychidae: a well developed ventral plate (Fig.3) bearing sensory setae which is joined to the glans basally and is apparently embryologically related to it; a mid-dorsal plate, similarly derived; and dorsolateral plates on each side embryologically related to the truncus.

It seems that Martens is correct in considering this penis configuration as plesiomorphic for the Triaenonychidae, and that various apomorphic configurations in the family can be derived by the

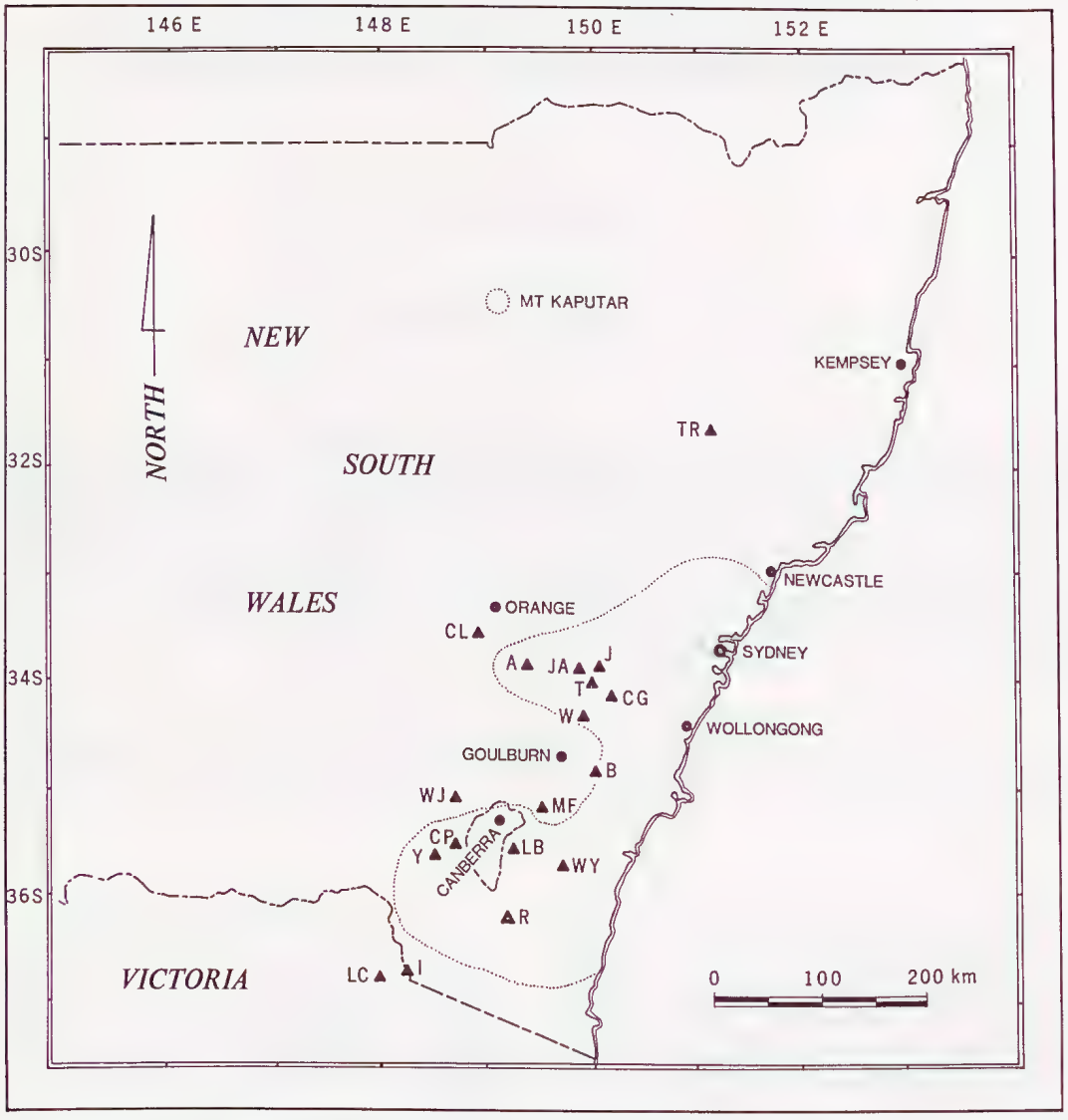

Fig.1. Distribution of *Holonuncia* in eastern Australia. Triangles depict cave areas (adapted from Matthews, 1985); A = Abercrombie; B = Bungonia; CG = Colong; CL = Cliefden; CP = Cooleman Plain; I = Indi; J = Jenolan; JA = Jaunter; L = Limestone Creek; LB = London Bridge; MF = Mount Fairy; R = Rosebrook; T = Tuglow; TR = Timor; W = Wombeyan; WJ = Wee Jasper; WY = Wyanbene; Y = Yarrangobilly. Dotted lines indicate approximate known distribution of surface species.

reduction or loss of one or more of these plates. He is not correct in implying that this plesiomorphic condition characterises Australian Triaenonychidae. The genus *Lomanella*, for example, shows extreme reduction in plates which parallels that in some North American and Japanese taxa (Hunt & Hickman, in press).

It is possible that the penis of *Holonuncia* and similar genera is the most plesiomorphic form for triaenonychids possessing the full complement of plates. The glans is relatively simple, lacking the accessory processes which occur in some other genera, for example *Cluniella* and *Mestonia*. The mid-dorsal plate is of relatively simple morphology compared with the elaborately folded structures typical of many genera like *Nunciella, Calliuncus* and *Leionuncia*. The ventral plate is generally of conservative form without the conspicuous modifications possessed by some taxa including *Cluniella ornata* Forster.

I have regarded possession of a ventral notch in calcaneus 1 of males as a strong generic character, but revision of *Holonuncia* has qualified this view, at least for this genus. Two species at the southern limits of distribution, namely *H. recta* n.sp. and *H. hamiltonsmithi* n.sp. (and a more problematic species from the Sydney region, *H. enigma*), lack a notch despite possessing synapomorphies indicating monophyly with other *Holonuncia* spp. Presence or absence of a notch is considered relevant at the species group level in *Holonuncia*.

Male genital morphology is normally useful in establishing species boundaries within a genus. *Holonuncia*, however, generally has a penis of conservative morphology making the task difficult for some species. Electrophoresis was used to help elucidate some boundaries (results reported and discussed at end of paper).

All populations of *Holonuncia* which inhabit caves show at least some degree of morphological modification to cave life. Such 'troglomorphies' include depigmentation, eye regression but not loss, leg attenuation, reduced sclerotisation, and reduction in size and number of dorsal spines/tubercles. *Holonuncia sussa* n.sp. from Colong Caves is the most highly troglomorphic species; *H. dewae* n.sp. from Wombeyan Cave, somewhat less so. These two species appear to be obligate cavernicoles, or troglobites.

Unlike the situation with *Hickmanoxyomma* (Hunt, 1990), *Holonuncia* frequently has surface representatives in the genus in close proximity to caves, a situation similar to that reported by Forster (1965) for New Zealand cavernicolous *Nuncia* and *Hendea*. Forster considered the cave populations to be different species from those on the surface. In *Holonuncia*, however, it was frequently difficult to judge whether cave populations were conspecific with adjacent or nearby surface populations. In these cases, conspecificity was assumed. Briggs (1971) recognised both surface and cave populations of the north American triaenonychid *Zuma acuta*, basing his judgement on the degree of morphological similarity when troglomorphic variations are excluded. It would be interesting to extend electrophoretic studies to quantify gene flow between surface and cave populations of *Holonuncia*. The potential exists to determine which surface species gave rise to the cavernicolous forms, and whether there have been multiple invasions of particular cave systems, as may be the case at Jenolan, Colong and Bungonia Caves.

Holonuncia Forster, 1955

Holonuncia Forster, 1955: 388.

Type species. *Holonuncia cavernicola* Forster, 1955 by original designation.

Diagnosis. Eyemound rising immediately behind anterior margin. Anterior margin with a few tubercles on each side, rarely naked. TA3 with mesial pair of enlarged tubercles or small spines; sternum long and thin, spiracles partly obscured by bridging tubercles of coxa IV, free lateral sclerites absent. Chelicera without a proximal boss. Pedipalp femur with a proximoventral, unevenly trifid spine, most distal or second most distal retroventral spine strong. Calcaneus of leg I of male usually with notch. Ventral plate of penis narrow, usually only slightly wider than glans, with 3 inferior and 1 (rarely 2) superior seta on each side; ventral plate with a proximal hollow in which bases of proximal inferior setae are usually set; mid-dorsal plate as wide as or narrower than glans, subequal to or shorter than ventral plate, weakly bifid, with terminal bifurcations not strongly curved and not supporting the glans laterally; glans with distodorsal denticles.

Redescription. Eyemound rising immediately behind anterior margin, rounded or canaliculate or with a short simple spine or tubercle. Anterior margin below with 5 inter-appendage projections; above with a few small tubercles on each side or rarely naked. Scutal groove distinct mesially; the 5 tergal areas marked by faint tergal grooves and by tubercles/granules or rows of same, mesial pair on TA3 largest. Ninth abdominal tergite fused with anal plate; free lateral sclerites absent. Sternum long and narrow; genital operculum rounded; spiracle abutting coxa IV and slightly obscured by bridging tubercles. First segment of chelicera without a proximal boss, with prodistal spine. Pedipalp usually much larger in male; femur with proximoventral trifid spine with main shaft and 2 weaker accessory processes; most distal or second most distal of retroventral spines strong, subequal to most proximal retroventral spine; 2 prodistal spines on both femur and patella; tibia with 3 or 4 retro- and 3 proventral spines; tarsus with 3 large pro- and retroventral spines; claw movable. Proximal fusion of coxae II and III marked by suture; coxa II with labial process; coxa I with distal proventral compound, but not clavate, spine. Leg femora armed only with small granules; calcanei less than 0.35 length

of astragalus; calcaneus I of male with notch or notch lacking, astragali with pseudosegmentation. Male tarsus I with 4-5 segments, female 3; distitarsi I and II with 2 and 3-4 segments; adult claw of legs III and IV with 1 pair of short lateral branches. Ventral plate of penis narrow, usually only slightly wider than glans, with 3 inferior and 1-2 superior setae on each side, median cleft depth 0.2-0.5 plate length; ventral plate with a proximal hollow, best seen in lateral view, in which bases of proximal inferior setae are usually set; mid-dorsal plate simple in form, subequal to glans in width, subequal to or shorter than ventral plate, weakly bifid, with terminal bifurcations not strongly curved and not supporting the glans laterally; glans with distodorsal denticles, lacking accessory processes.

Comments. *Holonuncia* is apparently closely related to *Equitius* Simon and *Paranuncia* Roewer, though some of the similarities in genital structure may be symplesiomorphies. Synapomorphies for *Holonuncia* are distodorsal denticles on the stylus, and the proximal hollow in the ventral plate.

Distribution. South eastern mainland Australia: known southern limit is Limestone Creek Caves in the Victorian Alps; northern limit in the coastal ranges is at Timor Caves near Murrurundi, New South Wales; outlier to the north-west in the Nandewar Ranges via Narrabri.

Key to Males of Species in Genus *Holonuncia* Forster

1. Calcaneus I with ventral notch (Fig.4,B-D) 2

—— Calcaneus I straight 11

2. Eyemound with a small median spine (Fig.9A) 3

—— Eyemound rounded, at most with small median granule 5

3. Notch in calcaneus 1 tiny (Fig.15K) ..... *H. kaputarensis* n.sp.

—— Notch in calcaneus 1 large 4

4. Penis ventral plate widest basally (Fig.10H); anterior margin of carapace with large spines tending to be directed forward (Fig.10A) ..... *H. katoomba* n.sp.

—— Ventral plate widest sub-distally (Fig.6G); spines on anterior margin not tending to be directed forward ..... *H. francesae* n.sp.

5. Anterior margin naked (Fig.5,A-B) ..... *H. sussa* n.sp.

—— Anterior margin with spines, tubercles or granules 6

6. Ventral plate with 2 superior setae on each side (Fig.12J) ..... *H. dispar* n.sp.

—— Ventral plate with 1 superior seta on each side 7

7. Notch in calcaneus I shallow, depth less than 0.3 remaining calcaneus width (Fig.11K); collected in Wee Jasper Caves ..... *H. weejasperensis* n.sp.

—— Depth of notch in calcaneus I greater than 0.3 remaining calcaneus width (Fig.4D); not collected in Wee Jasper Caves 8

8. Anterior margin usually with 2 tubercles or granules on each side; collected in Wombeyan Caves ..... *H. dewae* n.sp.

—— Anterior margin usually with more than 2 tubercles/ granules; not collected in Wombeyan Caves 9

9. Proximal retroventral spine on pedipalp tibia reduced to a blunt granule and retroventral spines 3 and 5 closer together than spines 1 and 3 (Fig.8E), spine 4 often lacking ..... *H. tuberculata* (Roewer)

—— Proximal retroventral spine small but usually not reduced to a granule and distance between spines 3 and 5 similar to 1 and 3 (Fig.7F), spine 4 usually present 10

10. Tarsus I usually with 5 articles (Fig.7H); stylus of penis narrowest subdistally (at about 0.7 stylus length) (Fig.7J) ..... *H. seriata* (Roewer) n.comb.

—— Tarsus 1 usually with 4 articles; stylus of penis narrowest at about 0.5 stylus length (Fig.3J) ..... *H. cavernicola* Forster

11. Tarsus 1 with 3 articles, carapace width less than 2 mm ..... *H. enigma* n.sp.

—— Tarsus 1 with greater than 3 articles, carapace width greater than 2 mm 12

12. Stylus very broad basally, very narrow subdistally (Fig.14J); collected in Limestone Creek Caves, Victoria ..... *H. hamiltonsmithi* n.sp.

—— Stylus only slightly broader basally than sub-distally (Fig.13F) ..... *H. recta* n.sp.

Holonuncia cavernicola Forster, 1955

Figs 2-4

Holonuncia cavernicola Forster, 1955: 389-390.

Type material. New South Wales, HOLOTYPE, male, KS6912 (old no. K13022), Jenolan Caves, 33°49'S 150°02'E, label "W.J.R. det.", no other data. PARATYPE male, KS6914 (old no. K12570), Jenolan Caves, no other data.

Additional material examined. Jenolan Caves: KS 5077, Chifley Cave (J-2M), on flowstone, M. Gray, 13 Dec. 1979, 2 juveniles; KS 17829, Imperial Cave (J-4M), M.R. Gray, 25 Oct. 1987, 1 female; KS 19033, Devils Coachhouse (J-165A), Jenolan Caves Fauna Survey, in thick litter in flood bypass to west side, G. Smith and L. Wheeler, 12 Dec. 1987, 1 male; KS 19048, Hennings Cave (J-39), entrance chamber, Jenolan Caves Fauna Survey, wandering over floor, G. Smith and L. Wheeler, 13 Dec. 1987, 1 female; KS 19049, Cerberus Cave, Jenolan Caves Fauna Survey, Cave Guides, May 1988, 1 male; KS 19050, McKeowns Hole (J-68), Jenolan Caves Fauna Survey, on old bat guano in lower section of cave, M. Gibian, 19 Mar. 1988, 2 juveniles; KS 21401, cave in Southern Limestone, B. Dew, 25 July 1964, 2M; KS 21402, small cave in Southern Limestone, Speleological Club, 26 Sept. 1970, 1 female; KS 21403, cave in Southern Limestone, on guano, B. Dew, 3 Sept. 1970, 1 male; KS 21404, Temple of Baal Cave (J-9M), under rock, dark zone, G.S. Hunt, 1970, 1 female; SAM, BS2184, Paradox Cave (J-48), E. Hamilton-Smith, 2 Jan. 1973, 2 juveniles; SAM BS2185, same data, 1 male. Boyd Plateau via Jenolan Caves (epigean): KS 21438, Mount Edwards, 33°59'S 150°03'E, under log, G.S. Hunt, Apr. 1971, 1 male; KS 23153, Mount Wiburd, 33°50'S 150°02'E, 1400 m, inside log, G.S. Hunt, 10 Jan. 1973, 1 male; KS 23154, Mount Wiburd, G.S. Hunt, 20 Sept. 1969, 1 female; KS 23155, Mount Wiburd, under log, G.S. Hunt, 6 June 1971, 2 males, 1 female; KS 23156, Budthingeroo Creek, 33°54'S 150°02'E, G.S. Hunt, 24 Feb. 1973, 1 female; KS 23157, Budthingeroo Creek, G.S. Hunt, 11 June 1971, 1 female; KS 23158, Mount Emperor, 33°59'S 150°08'E, G.S. Hunt, 11 Jan. 1973, 1 male; KS 23159, Mount Edwards, headwaters of Council Creek, 33°50'S 150°03'E, G.S. Hunt, 29 Jan. 1971, 1 male; KS 23160, Green Gully, 32°47'S 149°41'E, M.R. Gray, 18 June 1971, 2 female; KS 23161, Gillespies Lookout near Mount Boss, 33°11'S 152°24'E under log, G.S. Hunt, 5 Dec. 1971, 1 male. McKeown's Creek valley Jenolan Caves, 33°49'S 150°02'E (epigean): KS 21406, on surface under logs, G.S. Hunt, 15 Apr. 1972, 3 male; KS 23162, under wood beside creek, G.S. Hunt, 20 Sept. 1969, 1 juvenile. Cavernicolous material from Tuglow Caves (KS 23165, KS 23166, SAM BS 2008, BS2009) and epigean material from Mount Shivering, south of Kanangra Walls (KS 23163), Oberon Prison Farm (KS 23164), Mulgoa (KS 21416), and Glenbrook (KS 21417) are tentatively assigned to this species.

Diagnosis. Prominent notch in calcaneus I; anterior margin with at least 3 prominent tubercles on each side; stylus in ventral view narrowest at about 0.5 its length and expands gradually without marked subapical constriction, in lateral view terminal flexure short and thick.

Redescription. MALE (Jenolan Caves population). *Body:* SL 3.83-4.45 (4.24), CW 2.74-3.08 (2.91)(n=5). Background colour of dorsum orange; pigmentation pattern (KS17829) as figured, intensity highly variable in different specimens. Eyemound rising at about 50° from anterior margin, about 0.5 as high as long; rounded in profile, unarmed except at most for tiny granule; eyes reduced. Anterior margin with 3-5 tubercles on each side. TA3 with pair of mesial tubercles tending to enlarge to small spines in many specimens; distribution of other tubercles and granules as figured. Coxosternal region as figured; genital operculum longer than wide; spiracle partly obscured by coxa IV. *Chelicerae:* CSL 2.17-2.40 (2.31). Prodistal spine on first segment moderately large; second segment spines as figured. *Pedipalps:* PFL 2.51-2.96 (2.79). Gracile; ratio PF:CW 0.86-1.00 (0.93). Femur with row of 5 mediodorsal spines size order 4,3,2,5,1, largest in distal half; 5-6 retroventral spines size order 1,5,3,2=4,6. Proximal accessory denticle on proximoventral trifid spine moderately developed, distal denticle weak. Tibia with 4 retroventral spines, spine 1 about 0.5 length spine 2, spine 4 much greater than 0.5 spine 3. *Legs*: long, FIV 4.10-4.92 (4.31), ratio FIV:CW 1.39-1.98 (1.54); calcaneus long, ratio CI:AI 0.18-0.25(0.22). Tarsus IV dorsally with 2 large setae placed at about 0.25 and 0.75; lateral branches inserted at about 0.4 on claw; Tarsal formula: 4-rarely 5(2),11-15(3-4),4,4. *Genitalia:* ventral plate with 1 superior and 3 inferior setae on each side, about 1.7 as long as wide, slightly wider than base of stylus, median notch about 0.3 plate length and not reaching level of bases of inferior setae. Mid-dorsal plate reaching beyond bases of superior setae but not reaching level of distal margin of ventral plate; terminal cleft shallow, depth about 0.75 narrowest width of plate. Stylus basally about 0.8 ventral plate width, viewed ventrally tapers gradually to its narrowest point at about 0.5 its length, and expands gradually without a marked subapical constriction; in lateral view, distal flexure short and thick, width about 0.5 length; distodorsal denticles inconspicuous and not set in longitudinal grooves.

FEMALE. Similar to male except: body smaller, SL 3.47-3.76 (3.61)(n=5), CW 2.27-2.30 (2.29); pedipalps relatively shorter, PFL 1.97-2.01 (1.99), spines more slender, short spines longer, proximal accessory denticle of trifid spine weaker. Tarsal formula:3-4(2),9-15(3-4),4,4.

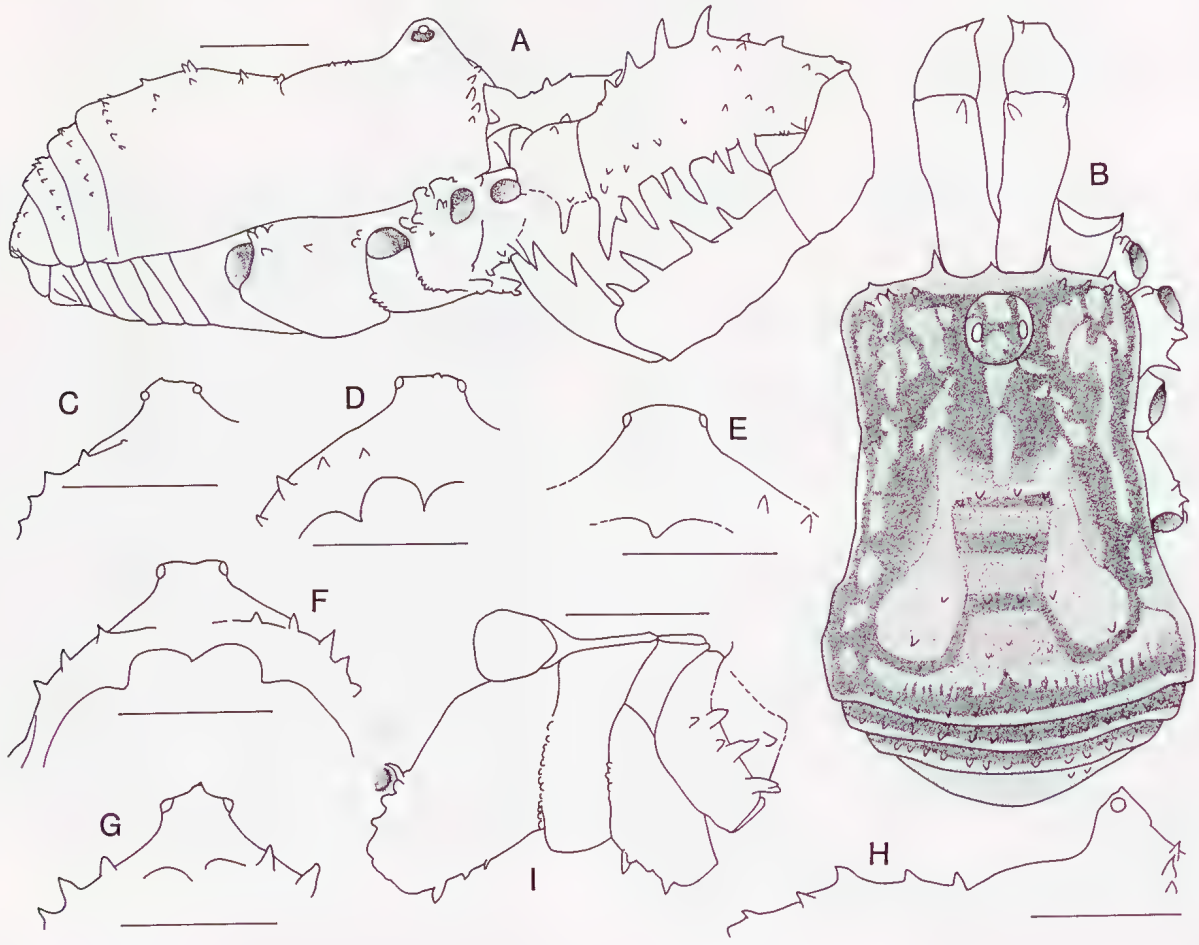

Fig.2. *Holonuncia cavernicola* Forster. A = body, lateral (KS19033); B = dorsum, relatively pigmented specimen, Imperial Cave, KS17829; C-G = eyemound and anterior spination, frontal; C-F = Jenolan Caves; C = holotype, D = KS19033, E = KS19049, F = KS17829, G = Mulgoa specimen, KS21416; Mulgoa specimen, lateral; I = coxisternal region, KS19033. All males. Scale bars = 1.0 mm.

Variation. Eyemound varies from canaliculate in a few specimens, rounded in most, to carrying a short spine in the Mulgoa population. Scute spination is subdued and legs relatively more elongate in holotype compared with most specimens. Mean relative leg length only slightly less for surface than for cave specimens. Pigmentation and eye size vary between cave and surface populations but also within the cave population(s).

Comments. One of Forster's male paratypes (K41749, Yarrangobilly Caves) lacks a notch in calcaneus I and belongs to *H. recta* n.sp. Surface populations at Jenolan and on the adjacent Boyd Plateau have an identical penis to cave populations of *H. cavernicola* and agree closely in other respects except eyes are normal in size and mean relative leg length is less (mean FIV:CW 1.30 compared to 1.54). These means are comparatively close, however the mean for the related *H. sussa* and *H. dewae* being respectively 2.35 and 2.09. Surface and cave populations of *H. cavernicola* are tentatively assigned to the same species. Variation in eyemound form noted above may indicate the presence of more than one species. For example, individuals at Jenolan Caves with a canaliculate eyemound may belong to a separate species

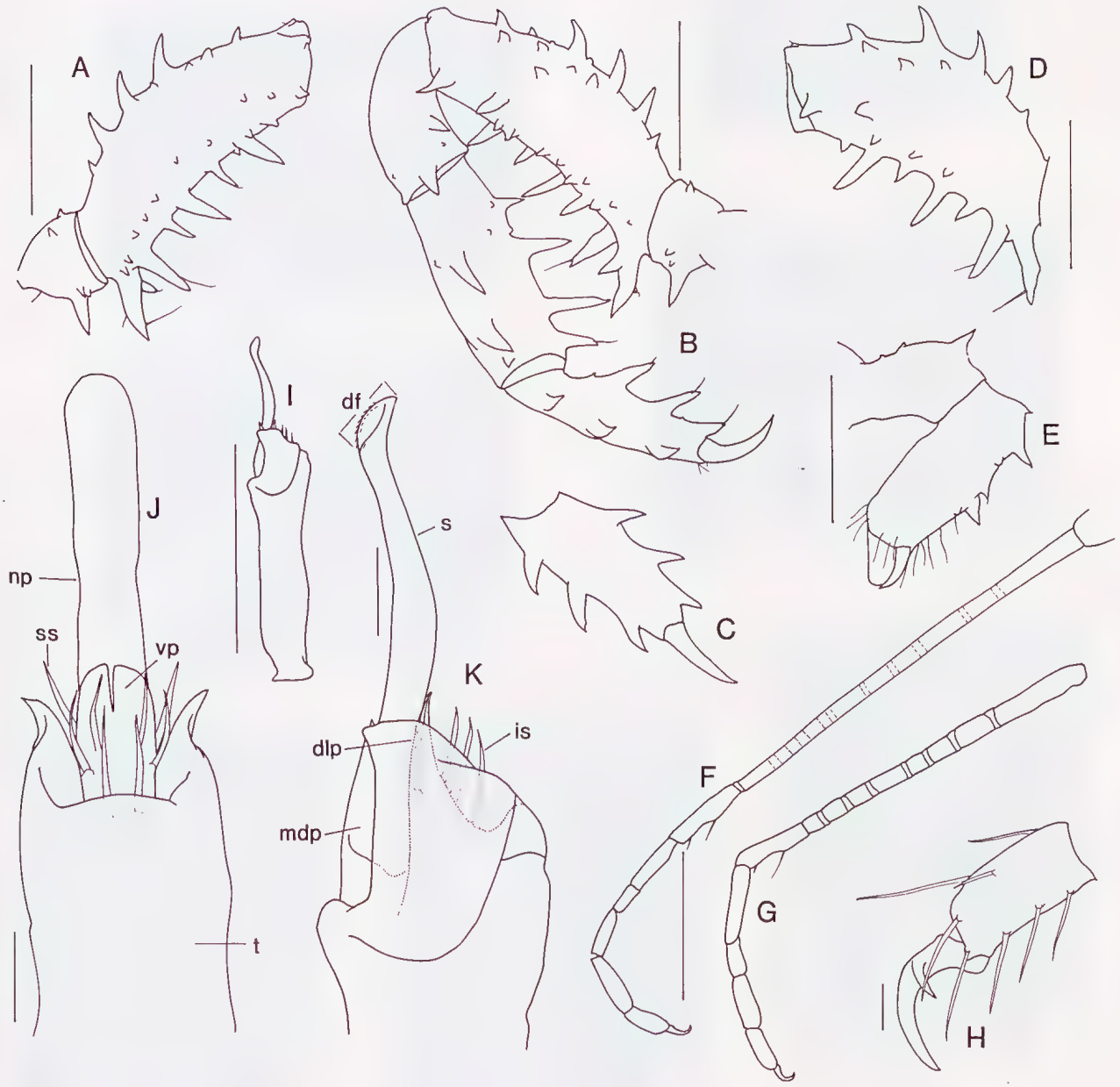

Fig.3. *Holonuncia cavernicola* Forster. D = female, others male; A-C, E-F = holotype. A = pedipalp femur, retrolateral; B = pedipalp, prolateral; C = pedipalp tarsus, ventral; D = pedipalp femur, prolateral, KS21402; E = chelicera, retrolateral; F-G = metatarsus and tarsus of leg I, retrolateral; G = epigean specimen, Boyd Plateau, KS21438; H = distal article of tarsus IV and claw with larger setae; I-K = penis, BS2185, I = entire, lateral, J = ventral, K = lateral. df = distal flexure, dlp = dorsolateral plate, is = inferior seta, mdp = mid-dorsal plate, np = narrowest point, s = stylus, ss = superior seta, t = truncus, vp = ventral plate. Scale bars: H, J-K = 0.1 mm, others = 1.0 mm.

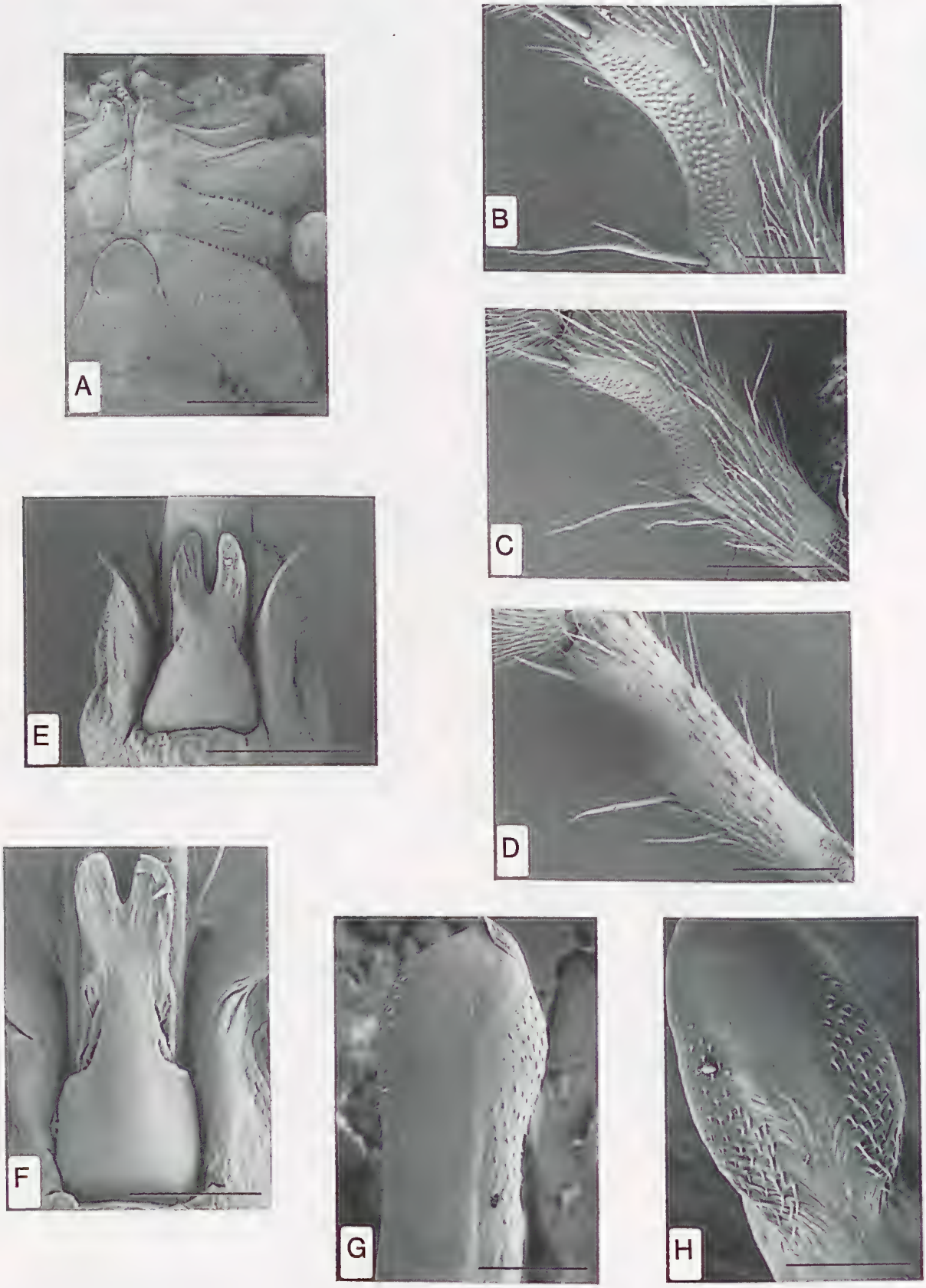

Fig.4. *Holonuncia* spp. A-C, F-G = *H. cavernicola Forster*; D-E, F = *H. seriata* (Roewer). A = coxisternal region; B-D = notch in calcaneus I, B = ventrolateral, C-D = prolateral; E-F = dorsal plate of penis; G-H = distodorsal denticles on stylus. Scale bars: A = 1.0 mm, B,F = 100 µm, C-E = 200 µm, G-H = 50 µm.

related to *H. sussa* which has such an eyemound. Allozyme electrophoresis would be useful in determining whether more than one species is present and whether gene flow occurs between cave and surface populations.

On the basis of penis form, *H. cavernicola* is most closely related to *H. sussa* and *H. dewae*.

Natural history. Cavernicolous individuals of *H. cavernicola* have usually been taken from the dark zone of caves. Surface individuals tend to be found deep in the core of large rotten logs (Hunt, 1979), in contrast to *Equitius doriae*, a common species in a related genus living in the same general habitat. *Equitius doriae* is easily found resting beneath even small logs and has never been collected beyond the entrance zone of caves. Surface populations of *H. cavernicola* may thus be 'preadapted' to cave life, or because of microhabitat preferences may have evolved in similar fashion to their cavernicolous relatives.

Distribution. New South Wales: Jenolan Caves area, both in caves and on the surface.

Holonuncia sussa n.sp.

Fig.5

Type material. New South Wales, Colong Caves: HOLOTYPE, male, AM KS 21439. PARATYPES: KS 21441, 1 female; KS21439, 2 females; SAM BS1292, K. Davey, 12 Jan. 1966, 1 male.

Diagnosis. Located in Colong Caves, eyemound 0.3 as high as long, eyes tiny, anterior margin without prominent tubercles or granules.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. SL 2.75-3.55(n=2), CW 1.97-2.34. Eyemound rising slightly behind anterior margin at an angle of about 30°, only about 0.3 as high as long, canaliculate and smooth, eyes tiny; anterior margin and carapace smooth, TA1-4 smooth, at most with 1 or 2 small mesial granules in each. CSL 1.56-1.98. PFL 1.92-2.24, ratio PFL:CW 0.97-1.00; pedipalp femur with 4 mediodorsal spines in proximal half size order 3=4,2,1, and 6 retroventral spines size order 1,3=5,2,4=6; proximal accessory denticle on trifid spine weak, distal lacking but its seta present; spine 1 on retroventral margin of tibia less than 0.5 spine 2. Legs relatively longer, FIV 4.97-5.10, ratio FIV:CW 2.18-2.52, mean ratio MI:CW 1.66, calcaneus relatively longer, mean ratio CI:AI 0.25; tarsal claw and its lateral branch very slender; tarsal formula 4(2),14-16(3-4),4,4. Genitalia very similar to *H. cavernicola*.

FEMALE. Differs from male as in *H. cavernicola*; small distal accessory denticle present on trifid spine; tarsal formula 3(2),12-13(3),4,4.

Comments. *Holonuncia sussa* is most closely related to *H. dewae* but differs in its low profile eyemound and lack of tubercles on the anterior margin. A female, probably of *H. cavernicola* or *H. seriata*, has also been collected in Colong Caves but is readily distinguished from *H. sussa* by its more heavily spined dorsum and larger eyemound and eyes. This sympatry supports the view that *H. sussa*, the most troglomorphic species in *Holonuncia*, is genetically isolated from its surface congeners.

Etymology. The specific epithet is a latinised acronym of the Sydney University Speleological Society (SUSS) which has been responsible for much of the exploration and early faunal studies of the Colong Cave system, and of which I have been a member for almost 30 years.

Natural history. The species is apparently a troglobite.

Distribution. New South Wales: Colong Caves.

Holonuncia dewae n.sp.

Fig.6

Type material. New South Wales, Wombeyan Caves, 34°06'S 150°08'E: HOLOTYPE male, KS 23168, Basin Chamber, Basin Cave (W-4). PARATYPES: Basin Cave: KS 23169, G.S. Hunt, 1 June 1964, 1 male, 7 females; KS 23170, B.B. Dew, Nov. 1963, 1 female; KS 23171, B.B. Dew, 18 Apr. 1964, 2 juveniles. Fig Tree Cave (W-148): KS 21437, G.S. Hunt, 2 June 1964, 1 male, 1 female; KS 23172, G.S. Hunt, 2 June 1964, 1 juvenile; KS 23173, on guano, 30 Oct. 1965, 1 female, 1 juvenile. Bullio Cave (W-2): KS 23174, on flowstone, G. Smith, 16 Sept. 1979, 1 male, SAM BS1261, E. Hamilton-Smith, 27 Feb. 1966, 4 males, 3 females

Diagnosis. Located in Wombeyan Caves, pale orange in colour, calcaneus I with prominent notch; anterior margin with at most 2 prominent tubercles; lateral branches of tarsal claw IV inserted at about 0.5 claw length.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. SL 3.31-4.18(3.68)(n=9), CW 2.34-2.86(2.54); body colour light orange with faint pigmentation pattern, slightly darker lateral to eyes; eyemound above eyes slightly conical, never canaliculate, eyes more reduced; anterior margin armed above with 2-3 tubercles/granules on each side, if 3 only 2 are conspicuous; tubercles/granules on dorsum slightly smaller. CSL 1.93-2.43(2.04). Pedipalps relatively longer, PFL 2.29-2.92(2.47), ratio PFL:CW 0.92-1.02(0.98). Legs relatively much longer, FIV 4.97-5.61(5.30), ratio

FIV:CW 1.82-2.40(2.09), metatarsi and tarsi very attenuated, mean ratio MI:CW 1.53; lateral branches inserted at about 0.5 length of tarsal claw of leg IV; tarsal formula 4(2),12-20(3),4,4. Stylus narrower basally, about 0.6 ventral plate width.

FEMALE. Differs from male as in *H. cavernicola*; CW 2.19-2.43(2.36)(n=4), PFL 1.92-2.16(2.05), FIV 4.88-5.12(5.02); tarsal formula 3(2),14-15(3),4,4.

Comments. The structure of the penis demonstrates that *H. dewae* is very closely related to *H. cavernicola* but differs from Jenolan cave specimens by the shape of the eyemound and tarsal claw on leg IV, and the tendency to have fewer tubercles/granules on the anterior margin and to have relatively longer legs. I had originally thought that the Wombeyan animals belonged in *H. cavernicola*. However, in addition to the slight morphological differences, it is probable that *H. dewae* is isolated from both surface and cave populations of *H. cavernicola*. *Holonuncia seriata* occurs in intervening country, at least at Mount Werong, and may well occur on the surface at Wombeyan.

Etymology. The specific epithet honours the late Miss Barbara Dew who was among the first Australian biospeleologists. It was on one of her field trips to Basin Cave, Wombeyan that I saw and collected my first

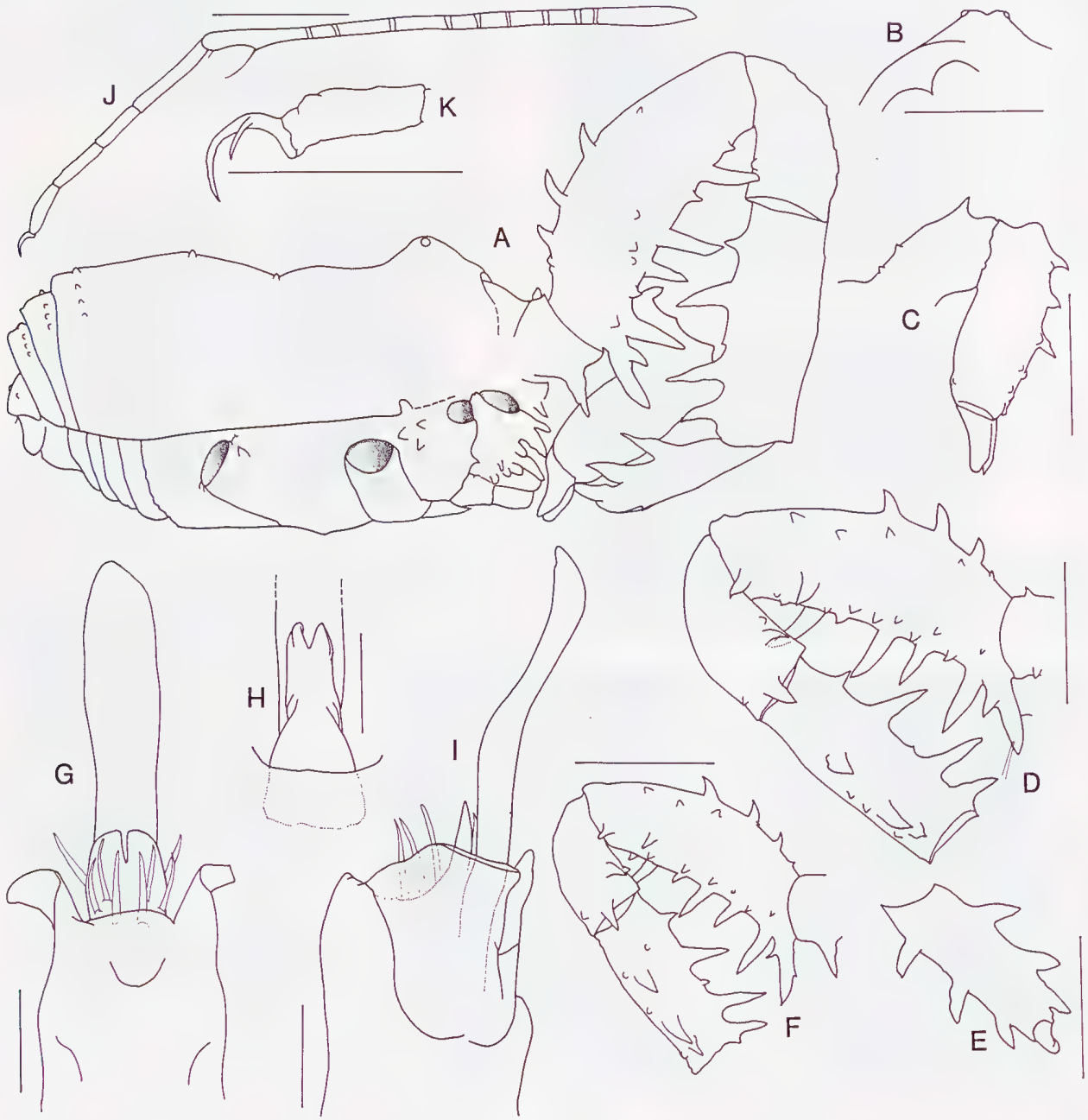

Fig.5. *Holonuncia sussa* n.sp. F = female, others male. A-E = holotype. A = body, lateral; B = eyemound, frontal; C = chelicera, retrolateral; D,F = pedipalp except tarsus, prolateral; E = pedipalp tarsus, ventral; G-I = penis, G = ventral, H = dorsal plate, I = lateral; J = metatarsus and tarsus of leg I, retrolateral; I = distal article of tarsus IV and claw. Scale bars: K = 0.5 mm, G-I = 0.1 mm, others = 1.0 mm.

harvestmen, an experience which led to my interest in the group.

Natural history. The species appears to be troglobitic.

Distribution. New South Wales: several caves at Wombeyan.

Fig.6. *Holonuncia dewae* n.sp. E = female, others male, KS21437. A = body, lateral; B = eyemound and anterior spination, frontal; C,E = pedipalp except tarsus, prolateral; D = pedipalp tarsus, ventral; F = chelicera, retrolateral; G-I = penis, G = ventral, H = dorsal plate, I = lateral; J = metatarsus and tarsus of leg I, retrolateral; K = distal article of tarsus IV and claw. Scale bars: G-I, K = 0.1 mm, others = 1.0 mm.

Holonuncia seriata (Roewer, 1915), n.comb.

Figs 4,7

Nuncia seriata, Roewer, 1915: 82-83.–Roewer, 1923: 593-4.

Type material. New South Wales: HOLOTYPE, female, Mount Murray, Roewer coll. no. 1020, no other data.

Additional material examined. New South Wales: Mount Murray near Robertson, 34°33'S 150°38'E: KS 19758, 650 m, closed forest, under rock, G.S. Hunt, 29 June 1987, 1 male; KS 19759, closed forest, under rotting wood, G.S. Hunt, 3 Jan. 1987, 2 females. The Gib, Mittagong, 34°05'S 149°56'E: KS 21408, under logs and rocks, G.S. Hunt, 24 Oct. 1987, 1 male, 2 females. Mount Werong, 34°05'S 149°56'E: KS 21436, near pluviometer, under logs, G.S. Hunt, 3 July 1972, 1 male; KS 21407, same data, 1 male, 2 juveniles. Plateau on Taralga Wombeyan Caves Road near Wombeyan, 34°22'S 149°49'E: KS 23175, under log, G.S. Hunt, 28 July 1989, 1 female. Bungonia Caves, 34°50'S 150°04'E: KS0648, Hogans Hole cave (B5), dark zone, D. Rothery, 15 Jan. 1977, 2 males; SAM BS0915, Fossil Cave (B4), B.P. Moore, 14 Mar. 1964, 2 males, 1 female. Other Bungonia Caves material is KS 21422, KS23180-3.

Redescription. MALE (Mount Murray, Mittagong population). Similar to *H. cavernicola* (cave population) except in following. Body slightly larger, CW 3.07-3.23(n=2), eyemound more elevated above eyes, eyes not reduced, tubercles/granules on TA1-5 slightly larger. CSL 2.70-2.87. Pedipalp and its spines more robust, PFL 2.94-2.99, ratio PF:CW 0.93-0.96; femur with row of 6 mediodorsal spines (size order 3=4,2,6,1=5) and 5 large retroventral spines (size order 1,5,3,4,2); spine 1 of tibia less than 0.5 length spine 2. Legs shorter, FIV 3.32-3.66, ratio FIV:CW 1.08-1.13; mean ratio MI:CW 0.91; calcaneus relatively longer, mean ratio CI:AI 0.33; tarsal formula: 5(2),11-12,4,4. Penis with ventral plate about 1.4 as long as wide, median notch about 0.25 plate length setae; mid-dorsal plate terminal cleft moderately deep, depth subequal to plate width; stylus viewed ventrally tapers gradually to narrowest point at about 0.7 its length, expands abruptly, is then constricted and expands apically; viewed laterally distal flexure long and narrow, width about 0.2 length; distodorsal denticles set in dorsolateral grooves.

FEMALE. Differs from male as in *H. cavernicola*. Tarsal formula: 3(2),10-13(3),4,4.

Variation. The Bungonia Caves population has relatively longer legs (mean FIV:CW 1.57 compared to 1.10), smaller eyes and less pigmentation than surface individuals.

Comments. Roewer (1915) sexes the type as a male, but it is a female. The population(s) in Bungonia Caves are tentatively assigned to this species. Electrophoretic study should help clarify relationships. A single female collected in Odyssey Cave has much longer legs than specimens from other caves. This cave is in a different limestone bed from most other caves in the Bungonia karst, connection being made below the water table by water flowing through fissures in intervening non-limestone strata (Jennings, 1972). It is therefore possible that this specimen represents a different, more troglomorphic species which is isolated from the other species in the Bungonia karst.

Specimens (KS23208, 21421, 19753-4) from the Budawang Ranges, south-west of Nowra, are morphologically very similar to *H. seriata*, but also resemble closely the specimens from Tomerong, near Nowra, which. on the basis of electrophoresis, probably represent a different species. The Budawang Ranges and Nowra are south of the Shoalhaven River while the type locality of *H. seriata* is to the north. Description of this putative new species will await further study of populations south of the Shoalhaven.

Distribution. New South Wales: plateaux country northwards from the Shoalhaven River to Mittagong and Mount Werong, both surface and caves.

Holonuncia tuberculata (Roewer, 1915)

Fig.8

Neonuncia tuberculata Roewer, 1915: 107-108.–Roewer, 1923: 605-6.
Holonuncia tuberculata.–Forster, 1955: 388, 390.

Type material. New South Wales: LECTOTYPE, male (here designated), New South Wales, Roewer coll. no. 1038, no other data, FIS. PARALECTOTYPE, female, same data, FIS.

Additional material examined. New South Wales: Royal National Park, 34°08'S 151°04'E: KS6666, Sydney University Zoology, 8 July 1972, 1 male, 1 juvenile; KS 21410, near Waterfall, under log, rainforest, S. McAuley, Apr. 1964, 1 male; KS 23177, Mascord Collection, R. Mascord, 2 July 1966, 1 female.

Diagnosis. Tarsus 1 of male with 4 segments, retroventral spines 3 and 5 on pedipalp close together (spine 4 may be lacking), retroventral spine 1 of pedipalp tibia reduced to a small granule.

Redescription. MALE. Similar to *H. cavernicola* (cave population) except in following. CW 2.48-2.72(n=4), eyes not reduced, pedipalp and its spines more robust, ratio PF:CW 0.77-0.88(0.83); femur with row of 6 mediodorsal spines size order 4,3,2,6,5,1 and 6 retroventral spines size order 5,1,3,2,4=6, spines 3 and 5 close together; retroventral spine 1 of tibia reduced to a granule. Legs shorter, FIV 2.67-3.5(3.01), ratio FIV:CW 1.08-1.12(1.10); mean ratio CI:AI 0.29; tarsal formula: 4(2),9-11(3),4,4. Penis with ventral plate about 1.7 as long as wide, median notch about 0.2 plate

length; mid-dorsal plate terminal cleft moderately deep, depth subequal to plate width; stylus viewed ventrally tapers gradually to narrowest point at about 0.7 its length and then expands apically, viewed laterally distal flexure long and narrow, width about 0.2 length; distodorsal denticles set in dorsolateral grooves.

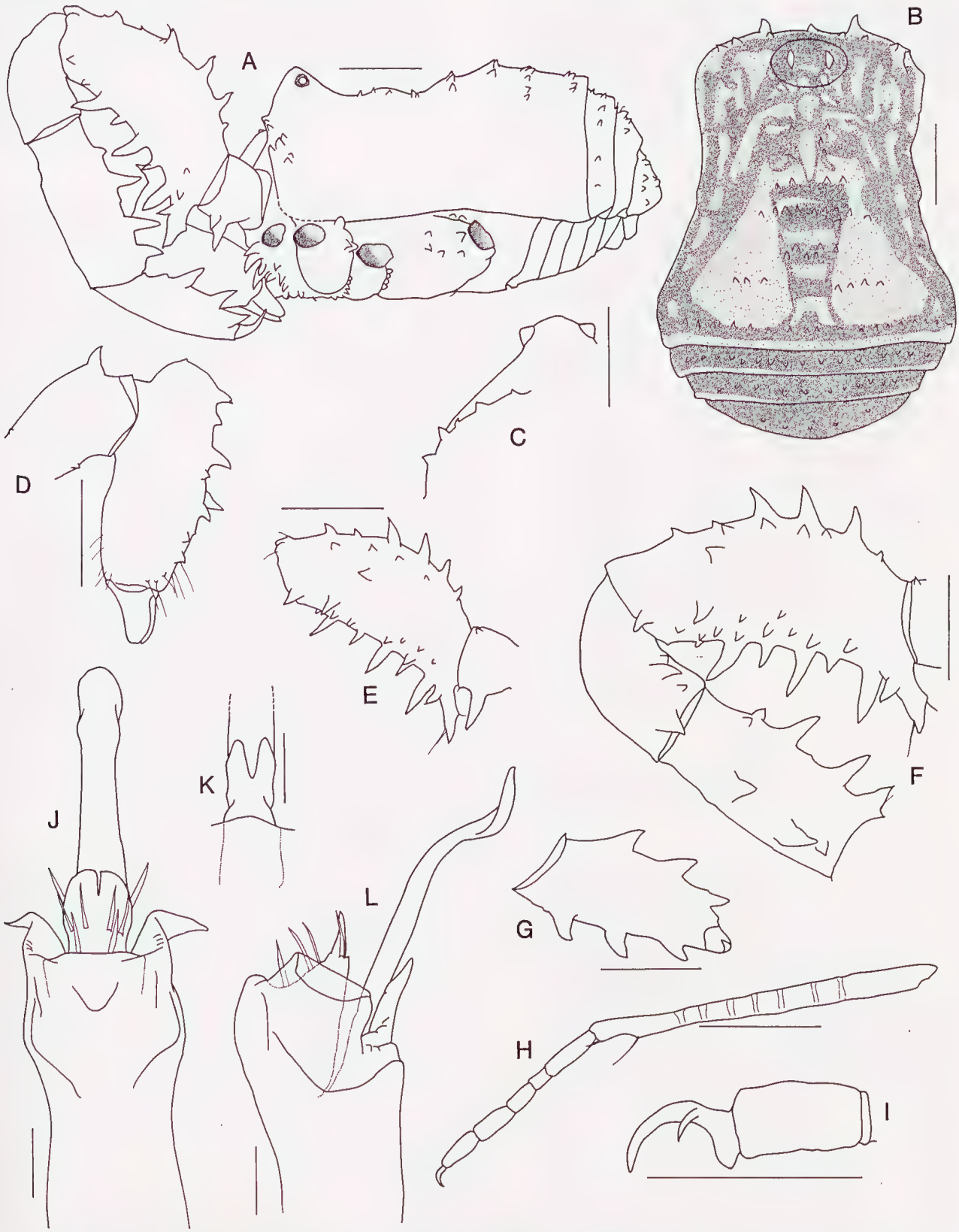

Fig.7. *Holonuncia seriata* (Roewer). E = holotype female, others male, KS19758. A = body, lateral; B = dorsum; C = eyemound and anterior spination, frontal; D = chelicera, retrolateral; E = pedipalp femur, prolateral; F = pedipalp except tarsus, prolateral; G = pedipalp tarsus, ventral; H = metatarsus and tarsus of leg I, retrolateral; I = distal article of tarsus IV and claw; J-L = penis, G = ventral, H = dorsal plate, I = lateral. Scale bars: I = 0.5 mm, J-L = 0.1 mm, others = 1.0 mm.

FEMALE. Differs from male as in *H. cavernicola* except that retroventral spine 1 on tibia remains granule sized in female. Tarsal formula: 3(2),10(3),4,4.

Comments. Forster (1955) placed this species in *Holonuncia* though he did not redescribe it. Roewer (1915, 1923) records the type locality as "Neu-Sud-Wales". Comparison of the lectotype male, particularly using pedipalp and genital structures, with specimens of known provenance indicates the species occurs in rainforest patches along coastal New South Wales between Port Hacking and the Shoalhaven River. This species differs from *H. seriata*, which occurs on plateaux areas immediately west of the coastal strip occupied by *H. tuberculata*, by the close spacing of retroventral spines 3 and 5 on the pedipalp femur, the small size of retroventral spine 1 on the tibia (though Mount Werong population of *H. seriata* has similar

Fig.8. *Holonuncia tuberculata* (Roewer). B,D = paralectotype female, A,J-K = KS6666, others lectotype male. A = body, lateral; B-C = eyemound and anterior spination, frontal; D = pedipalp except tarsus, retrolateral; E = pedipalp except tarsus, prolateral; F = chelicera, retrolateral,; G-I = penis, G = ventral, H = lateral, I = dorsal plate; J = metatarsus and tarsus of leg I, retrolateral; K = distal article of tarsus IV and claw. Scale bars: G-I = 0.1 mm, K = 0.5 mm; other = 1.0 mm.

condition for this latter character), and four rather than a usual five segments in tarsus I.

Distribution. New South Wales: Royal National Park and south to Jamberoo Mountain.

Holonuncia francesae n.sp.

Fig.9

Type material. New South Wales: HOLOTYPE, male, KS 14251, Gordon (Sydney suburb), 33 44'S 151 09'E, in litter, C Horseman, 28 Mar. 1984. PARATYPES: type locality: KS 10122, KS 10125, KS 10271, KS 10575, KS 10888, KS 12376, KS 12387, KS 12407, KS 12418, KS 12438, KS 12641, KS 13297, KS 13332, KS 13465, KS 13568, KS 13579, KS 13751, KS 14043, KS 14049, KS 14255, KS 14408, KS 14750, KS 21458, KS 23186, KS 23187, KS 23188, pit-trapping program, 1982-4, C. Horseman and M.R. Gray, total 20 males, 14 females. Pymble reserve, Blackbutt Creek 33°45'S 151°09'E: KS 23193, under wood, G.S. Hunt, 5 July 1970, 1 male, 1 female. St Ives beside Ku-ring-gai Creek, 33°44'S, 151°10'E: KS 23196, under rotting wood in bush, G.S. Hunt, 3 Aug. 1969, 3 males, 6 females; KS 21409, KS 23206, under wood and stones, moist conditions, G.S. Hunt, 26 July 1969, 1 male, 2 females, 9 juveniles. Killara, 33°45'S 151°10'E: KS 23197, beside Arterial Road, under wood, very moist, G.S. Hunt, 24 Aug. 1969, 1 male, 2 female; KS 23203, 76 Rosebery Road, under small rocks in moist conditions, G.S. Hunt, 15 June, 1964, 1 female; KS 23204, same data, 1 male, 2 females; Ryde, Malvina High School, 33°48'S 151°06'E: KS 23189, under sandstone, G.S. Hunt, 3 June 1970, 1 male, 1 female; KS 23190, under rock moist conditions at edge of bush, G.S. Hunt, 22 May 1969, 1 female; KS 23191, same data, 1 Apr. 1969, 1 male, 3 females. Willoughby, 33°47'S 151°13'E: KS 23192, in bush beside rubbish tip, under log, G.S. Hunt, 2 Aug. 1969, 1 male; KS 23205, Gore Creek, M.R. Gray, July 1988, 1 male, 1 juvenile. Mosman, 51 Parriwi Road, 33°50'S 151°15'E: KS 23194, in garden at base of bananas, G.S. Hunt, 9 Aug. 1964, 3 males; KS 23195, under rock, G.S. Hunt, 28 Mar. 1988, 1 male. Greenwich, beside Gore Creek, 33°54'S 151°11'E: KS 23198, in cavity in moist log, G.S. Hunt, 27 July 1969, 2 females; KS 23199, under bark at base of *Angophora*, G.S. Hunt, 10 Aug. 1968, 1 male; KS 23200, under rock, G.S. Hunt, 29 July 1969, 2 juveniles. Narrabeen, 33°44'S 151°18'E: KS 23201, Middle Creek, Wakehurst Parkway, rainforest, G.S. Hunt, 13 June 1970, 1 female; KS 6670, downstream from Oxford Falls, Wakehurst Parkway, rainforest, G.S. Hunt, 1 Feb. 1982, 2 males, 1 female. North Curl Curl, 33°47'S 151°18'E: KS 23202, F.J. Beeman, 19 Aug. 1956, 1 male. Bargo, 34°17'S 150°35'E: KS 21411, 17.5 km south of Pheasants Nest Bridge, under log, G.S. Hunt, 24 Oct. 1987, 1 male; KS 23213, Tea Tree Hollow, north boundary Wirrimbirra Sanctuary, under canopy of leaves of Black Bog Rush, D. Wilson, 16 Aug. 1969, 1 male; KS 23214, same data, G.S. Hunt, 16 Aug. 1969, 3 females. south side Razorback Ridge near Camden, 34°03'S 150°42'E: KS 23215, under moist rotting wood in rainforest-like conditions beside tributary Racecourse Creek, G.S. Hunt, 17 Aug. 1969, 1 male, 3 juveniles.

Other material examined. New South Wales: Blue Mountains National Park, 18 km east of Woodford, 33°44'S 150°33'E, KS 6667 low open forest heath, under logs, M.R. Gray, 17 Apr. 1974, 1 male, 1 female. Royal National Park, 34°08'S 151°04'E: KS 13818, beside creek near end of Wallamarra track, under logs, rainforest, G.S. Hunt, 10 Jan. 1984, 1 female; KS 21412, M.R. Gray, July 1970, 1 male. Bilpin, 33°30'S 150°31'E: KS 16565, G.S. Hunt, 12 May 1986, 1 male. Between Bilpin and Kurrajong Heights, 33°32'S 150°38'E: KS 21418, dry sclerophyll, 1 male, 1 juvenile. St Albans via Wisemans Ferry, 33°18'S 150°59'E: KS 21413, beside creek in hilly country, G.S. Hunt, 20 Dec. 1969, 1 male. Watagan Mountains, 32°57'S 151°14'E: KS 21414, G.S. Hunt, no date, 2 male.

Diagnosis. Calcaneus I with notch, eyemound with short spine, largest mediodorsal spine on pedipalp femur in distal half, ventral plate of penis widest subdistally.

Description. MALE. Similar to *H. cavernicola* (cave population) except in following. Mean body size slightly smaller, CW 2.51-3.03(2.84)(n=5). Eyemound armed with a short spine; eyes not reduced. CSL 2.17-2.66(2.40); second segment of chelicera more spinose distodorsally. PFL 2.25-2.90(2.67), PFL:CW 0.87-0.98(0.92); pedipalp femur with 5-6 mediodorsal spines size order 5,4,3,6,2,1 and 5 retroventral spines size order 1=5,3,2,4; distal accessory denticle on trifid spine relatively strong; retroventral spine 1 on tibia less than 0.5 spine 2. FIV 3.84-4.40, FIV:CW 1.36-1.53(1.45), mean CI:AI 0.26; tarsal formula 4-5(2),10-12(3),4,4. Genitalia very similar to *H. seriata*.

FEMALE. Differs from male as in *H. cavernicola*; tarsal formula 3(2),9-10(3),4,4.

Variation. The shape of the dorsal plate varies (Fig.9I-K). The ventral plate cleft is somewhat deeper in the St Albans specimen.

Comments. The species is closely related to *H. seriata* and *H. tuberculata* but differs in having a spine on the eyemound.

A specimen carrying a spine on the eyemound and occurring south of the Shoalhaven River (near Nowra) is electrophoretically more similar to *H. francesae* from the Sydney region than the specimens without a spine with which it is in sympatry. Specimens bearing the spine also occur further south, for example, KS3842 and KS 2620 from Kioloa State Forest near Batemans Bay. The Shoalhaven River has proved a significant barrier for some taxa, for example in the related genus *Equitius* (Hunt, 1985). Populations south of the Shoalhaven and carrying an eyemound spine are considered to belong to a new, as yet undescribed species, with affinities to *H. francesae* whose distribution lies well to the north of the River. This undescribed species is sympatric with another undescribed species resembling *H. seriata* (see allozyme electrophoresis discussion below).

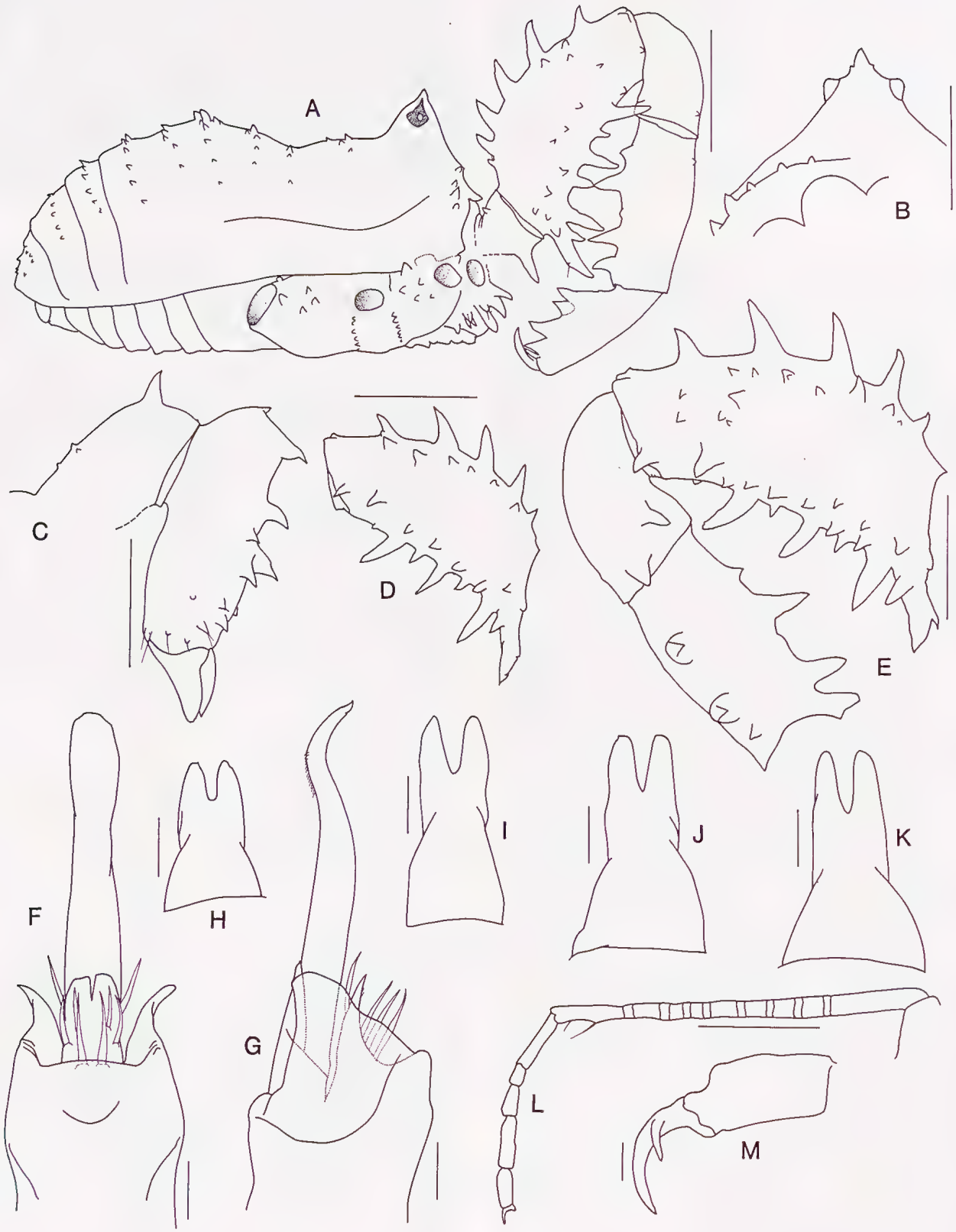

Fig.9. *Holonuncia francesae* n.sp. D = female, KS14750, A = holotype male, F-H = male, KS13332, others = male, KS13579. A = body, lateral; B = eyemound and anterior spination, frontal; C = chelicera, retrolateral; D = pedipalp femur, prolateral; E = pedipalp except tarsus, prolateral; F-H = penis, F = ventral G = lateral, H = dorsal plate; I-K = dorsal plate *ex* Pheasants Nest Bridge near Bargo, Saint Albans and Wattagan Mountains; L = metatarsus and tarsus of leg I, retrolateral; M = distal article of tarsus IV and claw. Scale bars: F-K, M = 0.1 mm, others = 1.0 mm.

Etymology. The specific epithet acknowledges the patience of my wife, Frances, whose support has made much of my research possible. Appropriately, the species occurs in our semi-natural garden in Mosman, a suburb of Sydney.

Natural history. In an extensive pit-fall sampling program at the type locality, males outnumbered females by approximately 4 to 1, indicating they were more ambulatory. This may be associated with reproductive activity.

Distribution. New South Wales: Sydney region, from Royal National Park in the south to Watagan Mountains in the north, and westwards to Bargo, and to Woodford and Bilpin in the Blue Mountains.

***Holonuncia katoomba* n.sp.**

Fig.10

Type material. New South Wales, Katoomba, 33°43'S 150°19'E: HOLOTYPE, male, KS 21415, no other data; PARATYPE, male, KS 23179, no other data.

Diagnosis. Notch in calcaneus I of male prominent, eyemound with a small spine, anterior margin with 7-8 tubercles/granules on each side which tend to be directed forward, ventral plate of penis widest basally.

Description. MALE. Similar to *H. cavernicola* (cave population except in the following. Body larger, CW 2.64-3.06(n=2). Eyemound armed with a short spine, eyes not reduced; anterior margin armed with 7-8

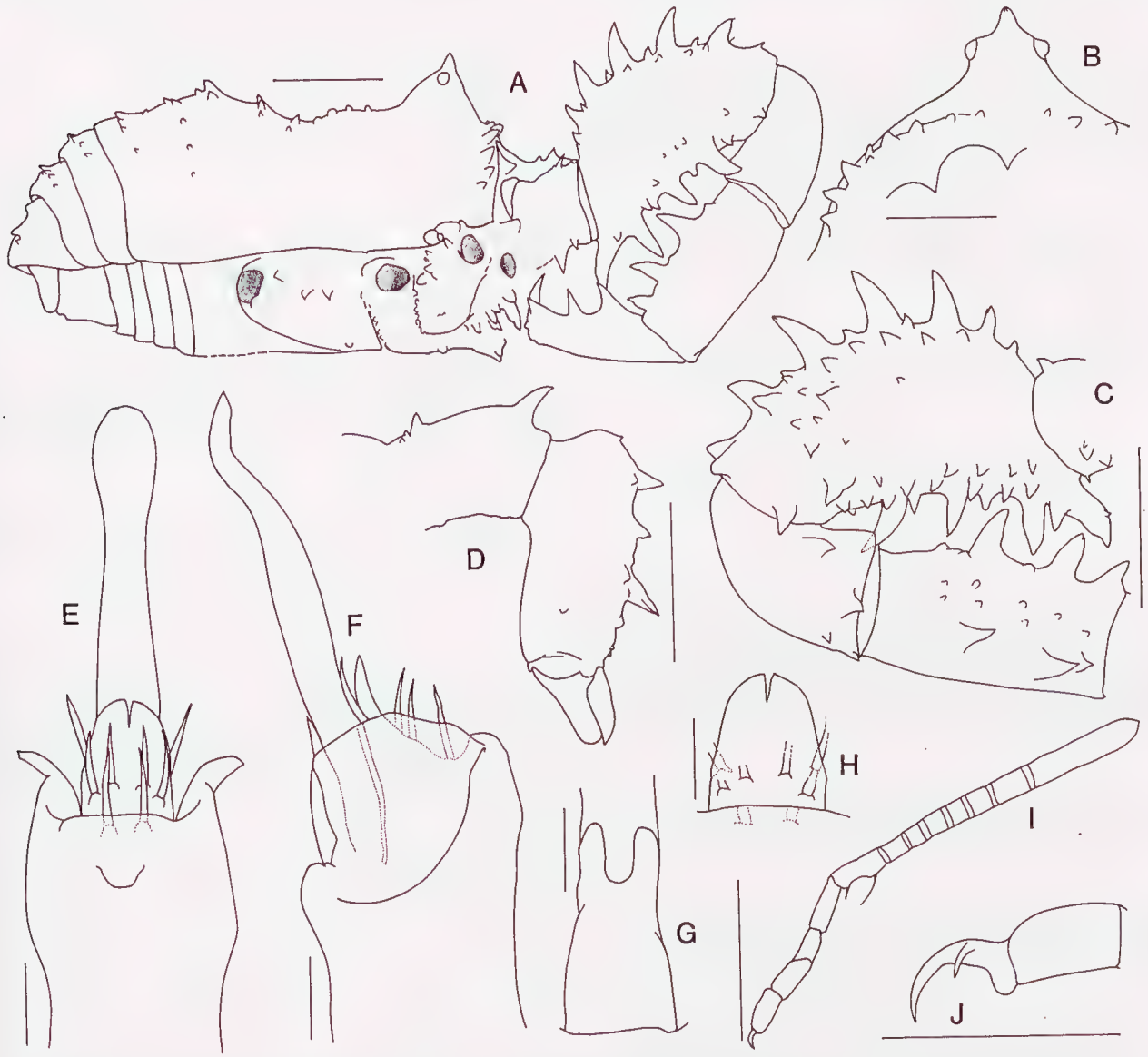

Fig.10. *Holonuncia katoomba* n.sp. A-G = holotype male; H-J = male, KS21415. A = body, lateral; B = eyemound and anterior spination, frontal; C = pedipalp except tarsus, prolateral; D = chelicera, retrolateral; E-G = penis, E = ventral, F = lateral, G = dorsal plate; H = ventral plate shape; I = metatarsus and tarsus of leg I, retrolateral; M = distal article of tarsus IV and claw. Scale bars: E-H = 0.1 mm; J = 0.5 mm; others = 1.0 mm.

tubercles/granules on each side which tend to directed forward. Mesial spines on TA3 larger. CSL 1.98-2.19, second segment robust, mid-dorsal spine much longer than proximodorsal spine. Pedipalp femur short and robust, PFL 2.27-2.47, PFL:CW 0.81-0.86; femur with 5-6 mediodorsal spines size order 5,4,3,6,2,1; 5 retroventral spines size order 1 or 5,3,2=4; proventral surface more spinous; spine 1 on tibia reduced to granule, venter of tibia granular. Legs short, FIV 3.06-3.23, FIV:CW 1.06-1.16; mean CI:AI 0.23; tarsal formula 4(2),9-10(3),4,4. Ventral plate of penis broadest basally, 1.5 as long as wide, 1.5 wider than base of glans, median cleft shallow, about 0.2 plate length; mid-dorsal plate cleft wide but depth only about 0.66 width of plate; stylus viewed ventrally tapers to narrowest point at about 0.75 its length and distally expands smoothly, viewed laterally distal flexure long, width about 0.2 its length; distodorsal denticles set in dorsolateral grooves.

Comments. *Holonuncia katoomba* has a localised distribution near the western periphery of the range of *H. francesae*, the species to which it is closely related. It differs in a more spinose anterior margin, and in the shape of the ventral and dorsal plates.

Etymology. The specific epithet is a noun in apposition and is the name of the type locality, Katoomba.

Distribution. New South Wales: Katoomba, Blue Mountains.

Holonuncia weejasperensis n.sp.

Fig.11

Type material. New South Wales, Wee Jasper Caves, 35°08'S 148°40'E: HOLOTYPE, male, ANIC, Humidicrib Cave (WJ-34), E. Holm, 19 May 1987. PARATYPES: KS 1531, Dip Cave (WJ-1), dark zone, M. Marx, 7 May 1978, 1 male, 1 female; KS 16256, cave 6.5 km south of Wee Jasper, J.H. Webb, 4 Jan. 1956 1 male.

Diagnosis. Wee Jasper Caves, notch in calcaneus I shallow, pedipalp femur with 6 mediodorsal spines.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. Body tends to be smaller, CW 2.3 (n=1). CSL 1.90. PFL 2.27, PFL:CW 0.99; femur with 6 mediodorsal spines size order 3=4,2,1=5=6 and 6 retroventral spines size order 1=3=3,2 or 4,6. Legs tend to be relatively longer, FIV 4.00, FIV:CW 1.74, calcaneus relatively longer CI:AI 0.29, notch in calcaneus I long and shallow; lateral branches on tarsal claw of leg IV inserted at about 0.5 claw length; tarsal formula 4(2),11-13,4,4. Ventral plate of penis about 1.3 as long as wide, median notch deep, about 0.5 plate length. Dorsal plate terminal cleft moderately deep, depth subequal to plate width; stylus similar to *H. seriata*.

FEMALE. Differs from male as in *H. cavernicola*. Tarsal formula: 3(2),12-17(3),4,4.

Comments. *Holonuncia weejasperensis* is closely related to *H. seriata* which occurs in surface and cave habitats in the coastal ranges north-east of Wee Jasper. It differs from cavernicolous *H.seriata* in having a long, shallow notch in calcaneus of leg I. Humidicrib cave was chosen as the type locality as there has been research on its bat colony (Hall *et al.*, 1975) and it is less subject to recreational use than Dip Cave.

Etymology. The specific epithet refers to Wee Jasper Caves in which the species occurs.

Natural history. The species appears to be a troglobite.

Distribution. New South Wales: Wee Jasper Caves.

Holonuncia dispar n.sp.

Fig.12

Type material. New South Wales, Budawang Ranges, Quiltys Mountain, 35°22'S 150°03'E. HOLOTYPE, male, KS21419, under rocks in rainforest beside Kilpatrick Creek, eastern side of mountain, G.S. Hunt, 17 Apr. 1969. PARATYPE, female, KS 21435, same data.

Diagnosis. Notch in calcaneus I of male shallow; ventral plate of penis wide, almost twice as wide as base of glans, and equipped with 2 superior setae.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. SL 3.85. Colour pattern of dorsum has faded in preservation. Eyemound shortly conical in anterior view, eyes not reduced. Anterior margin with smaller tubercles; granules on carapace posterior to eyes lacking; mesial tubercles on TA3 smaller; genital operculum more round. CSL 2.45. Pedipalp and its spines more robust, PFL 2.70; size order mediodorsal spines on femur 3=4,2,1,5, size order retroventral spines 5,1=3,2,4; proximal retrolateral spine on tibia blunt. Legs relatively short; notch in calcaneus shallow; tarsal formula 4(2),12(3),4,4. Ventral plate of genitalia with 2 superior and 3-4 inferior setae, about as wide as long, almost twice as wide as base of glans, notch about 0.25 plate length; mid-dorsal plate terminal cleft moderately deep, depth subequal to plate width; stylus viewed ventrally with apical expansion more clearly defined, viewed laterally wider basally, distal flexure long and narrow, width about 0.25 length; distodorsal denticles

set in dorsolateral grooves; dorsolateral plate broad distally.

FEMALE. Differs from male as in *H. cavernicola*. Carapace with 2 granules posterior to eyes; calcaneus of similar length to that in male; tarsal formula 3(2),11(30,4,4).

Comments. The affinities of this species are uncertain but, on the basis of stylus shape, it appears more closely related to *H. seriata* than to *H. cavernicola*. The male is readily separated from *H. seriata* by the shallow notch and the two superior setae on the penis ventral plate. It is sympatric with a species of *Holonuncia* which is similar morphologically to, but distinct electrophoretically from, *H. seriata*. Females of *H. dispar* cannot be differentiated with certainty from this sympatric species. Because *H. dispar* appears to be rare, an unusual female having a calcaneus of similar length to the male was selected as a female for this species. Verification of this choice is needed.

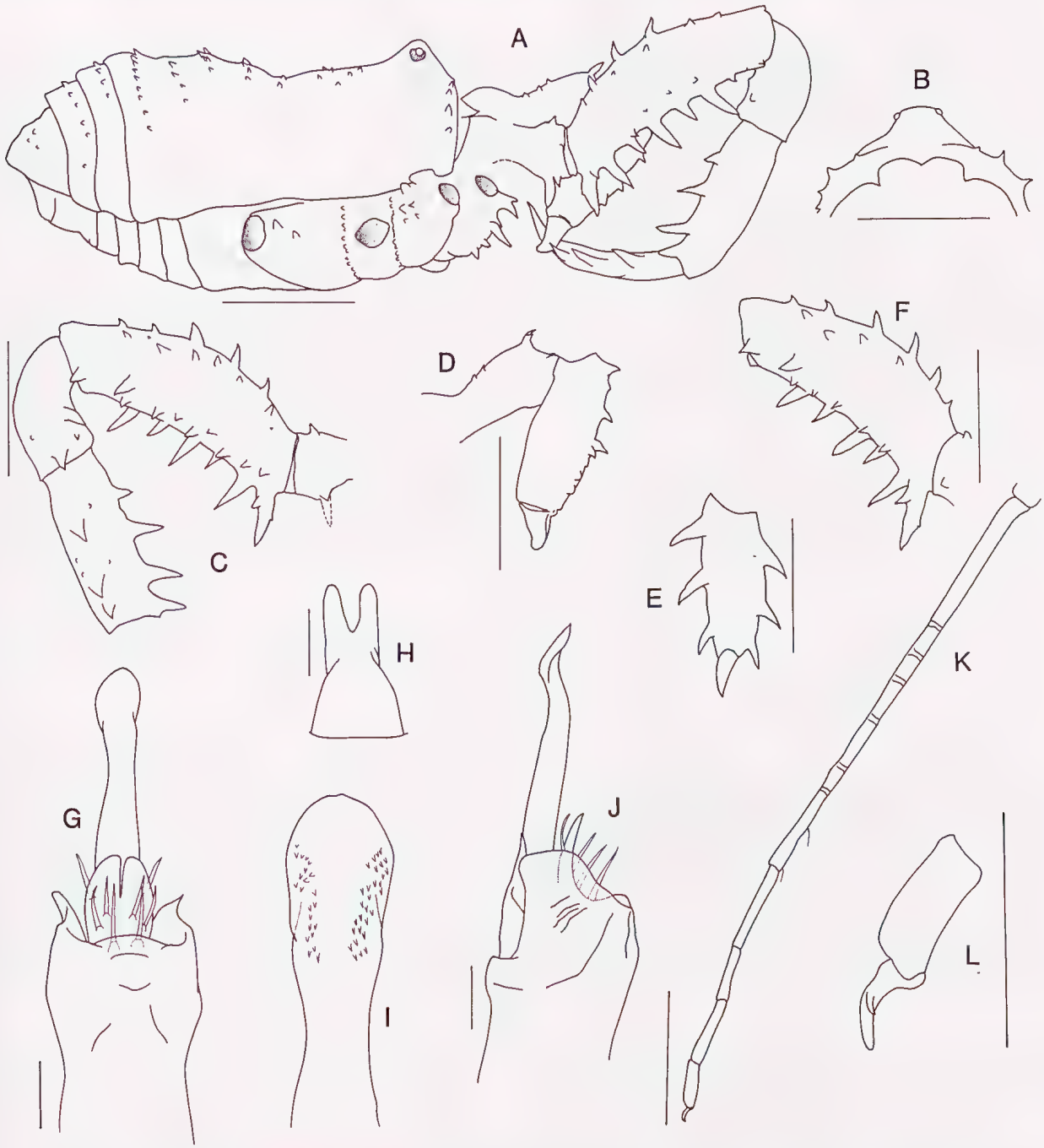

Fig.11. *Holonuncia weejasperensis* n.sp. F = female; others = holotype male. A = body, lateral; B = eyemound and anterior spination, frontal; C = pedipalp except tarsus, prolateral; D = chelicera, retrolateral; E = pedipalp tarsus, ventral; F = pedipalp femur, prolateral; G-J = penis, G = ventral, H = dorsal plate, I = distodorsal part of stylus; J = penis, lateral; K = metatarsus and tarsus of leg I, retrolateral; L = distal article of tarsus IV and claw. Scale bars: G-H,J = 0.1 mm, I = terminal part of G enlarged; L = 0.5 mm, others = 1.0 mm.

The asymmetrical presence, in the single male available, of four inferior setae on one side of the ventral plate and the usual three on the other suggests the possibility that the presence of two superior setae, albeit symmetrical, may be due to a somatic abnormality. However, the shallow notch and the fact that two superior setae is a consistent character in some species of the closely related *Hickmanoxyomma* (Hunt, 1990) suggest that *H. dispar* is a valid species and not an abherrent form of the more common species in sympatry with it.

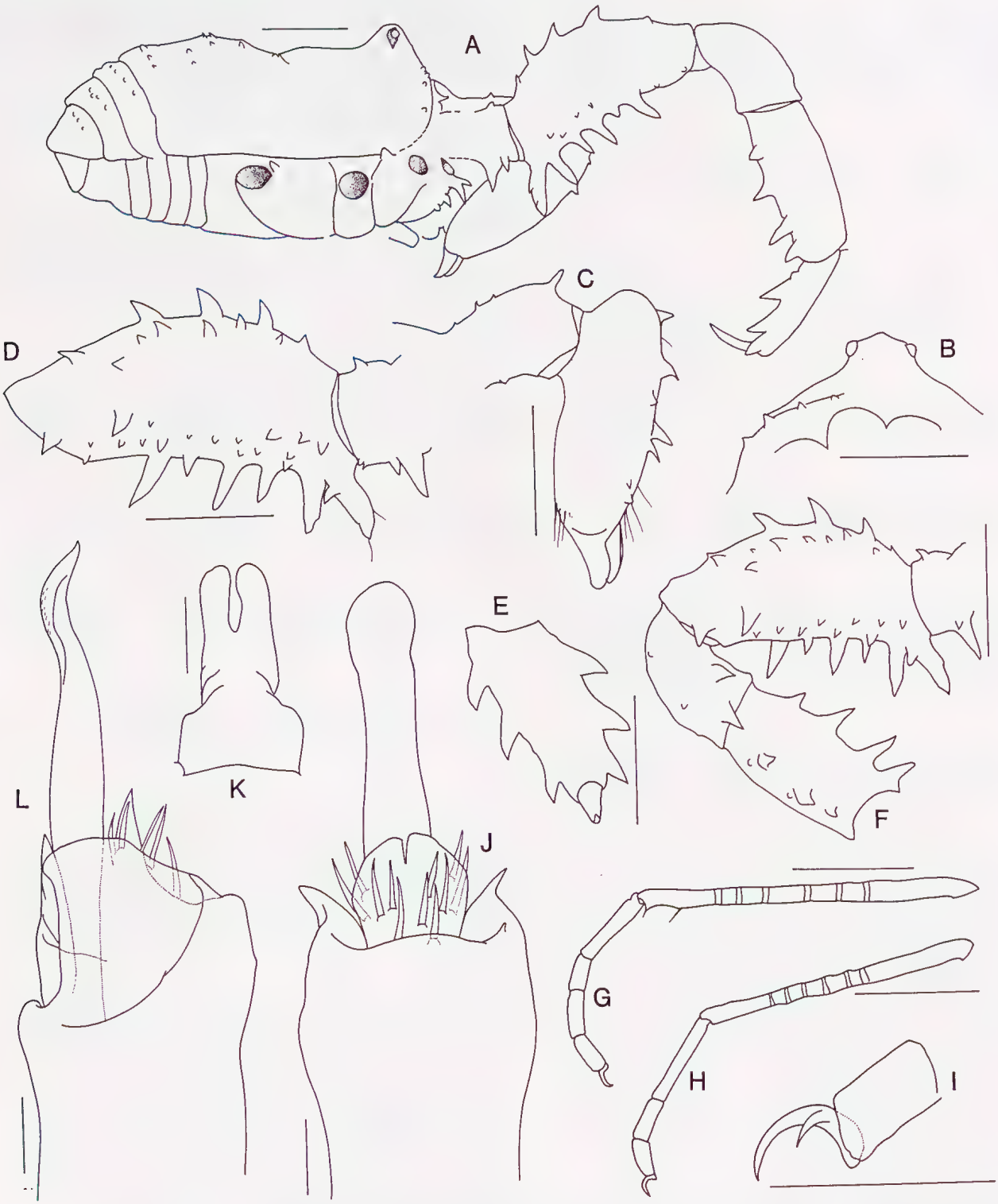

Fig.12. *Holonuncia dispar* n.sp. F,H = female, KS21435; others = holotype male. A = body, lateral; B = eyemound and anterior spination, frontal; C = chelicera, retrolateral; D = pedipalp femur, prolateral; E = pedipalp tarsus, ventral; F = pedipalp except tarsus, prolateral; G-H = metatarsus and tarsus of leg I, retrolateral; I = distal article of tarsus IV and claw; J-K = penis, J = ventral, K = dorsal plate, L = lateral. Scale bars: J-L = 0.1 mm, I = 0.5 mm, others = 1.0 mm.

Etymology. The specific epithet refers to the unusual male genital features of this species.

Distribution. New South Wales: rainforest at the base of Quiltys Mountain, Budawang Ranges.

Holonuncia recta n.sp.

Fig.13

Type material. Australian Capital Territory: HOLOTYPE, male, KS21426, Mount Murray, near Jacks Creek just upstream of Yaouk Trail, open eucalypt forest, under log, 800 m, G.S. Hunt, 21 Apr. 1987. PARATYPES: KS14327, Tidbinbilla Nature Reserve, M. R. Gray, 9 Mar. 1978, 1 male; KS21427, same data, 1 female; KS21429, same data, 1 female; ANIC, Blundels, F. J. Gay, 7 Mar. 1958, 1 male; Bulls Head, under log, 19 Nov. 1958.

Other material examined. New South Wales: Yarrangobilly Caves, 35°43'S 148°30'E: Paratype male *H. cavernicola*, KS 6913. Stead. KS5703, Grotto Cave (Y-30), K. Keck, 3 Jun. 1980, 1 female; KS23211, cave, G. Butler, June 1957, 1 female; Eyrie Cave (Y-3E), M.R. Gray, 31 Oct. 1980, 1 male; SAM BS1912, un-named cave, G. Middleton, 27 Jan. 1970, 2 males; KS23212, on surface, near creek behind 'power house', under log, G.S. Hunt, 4 Apr. 1988, 1 female. Cooleman Plains: River Cave (CP-6), G. Smith, 15 Apr. 1979, 1 female. ?London Creek: ANIC, label indistinct, 1 male. Brown Mountain: ANIC, rainforest, berlesate no. 24, about 800 m, R.W. Taylor and R.J. Bartell, 11 Apr. 1967, 1 male.

Diagnosis. Calcaneus I without notch, carapace width greater than 2 mm, stylus without strong expansion near its base.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. Body large, CW 3.18-3.57(3.32)(n=4). Eyemound tends to slope more gradually posteriorly than anteriorly, eyes not reduced; genital operculum about as wide as long. CSL 2.68-3.05(2.89), dorsal spines and tubercles on second segment strong, spine placed at about 0.3 strong. PFL 3.01-3.60(3.28), ratio PFL:CW 0.95-1.01(0.99). Pedipalp femur with row of 6 mediodorsal spines size order 3=4,2,1,5=6; size order of retroventral spines 1=3=5,2,4; proximal accessory denticle on trifid spine strong; prolateral surface more spinose; retroventral spine 1 on tibia less than 0.5 length spine 2, proventral spine 3 weak, less than 0.5 length spine 2. Legs relatively short, FIV 3.86-4.46(4.24), ratio FIV:CW 1.21-1.33(1.26), mean MI:CW 0.98; calcaneus I without notch, mean CI:AI 0.27; tarsal formula 4(2), 10-15(3),4,4. Genitalia similar to *H. seriata*.

FEMALE. Differs from male as in *H. cavernicola* except that calcaneus 1 without conspicuous dimorphism; tarsal formula 3(2),9-11(3),4,4.

Variation. The specimens from Yarrangobilly Caves are smaller, CW 2.68-3.17(2.85)(n=4), and show some troglomorphy including eye reduction and leg attenuation, FIV:CW 1.70-1.81(1.76). The median cleft in the ventral plate is deeper, about 0.5 plate length and the plate is somewhat broader. The surface specimens from Brown Mountain to the east tend to have a prominent flange on the dorsolateral plate. The specimen from London Creek has a slightly canaliculate eyemound.

Comments. This species appears most closely related to *H. hamiltonsmithi* which also lacks a notch and inhabits the same general region of Australia. It differs from the latter species in spination of the anterior margin and the shape of the stylus. Despite having a straight calcaneus I, *H. recta* also appears closely related to *H. seriata* and *H. weejasperensis*.

The differences between surface populations and the cave populations at Yarrangobilly are suggestive of genetic isolation and perhaps specific difference. Allozyme work would help resolve this problem. KS21425 from Piccadilly Circus, Brindabella Range, has a notch in calcaneus I and belongs to a different species. As the male genitalia were lost, the species remains undescribed.

Etymology. The specific epithet refers to the straight calcaneus I of the male.

Distribution. South-east New South Wales and Australian Capital Territory.

Holonuncia hamiltonsmithi n.sp.

Fig.14

Type material. Victoria, Limestone Creek Caves, 36°50'S 148°05'E. HOLOTYPE, male: SAM N1992233, Sheehans Cave (LC-5), E. Hamilton-Smith, 11 Mar. 1972. PARATYPES: SAM, same data, 1 female; SAM BS2205, Cave LC-1Q, E. Hamilton-Smith, 11 Mar. 1972, 2 females.

Diagnosis. Limestone Creek Caves, calcaneus I without notch; glans very broad above base, very narrow subapically.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. Body (1 specimen) smaller, CW 2.24. Eyemound rising at about 45° from slightly behind anterior margin, armed with a very short spine; anterior margin unarmed above except for 3 small granules; genital operculum about as wide as long. CSL 1.74. PFL 1.86, PFL:CW 0.83. Pedipalp femur with row of 6 mediodorsal spines size order 4,3,2,1,5=6; size order of retroventral spines 1,3=5,2=4; distal accessory denticle on trifid spine lacking; retroventral spine 1 on tibia weak, 0.5 spine

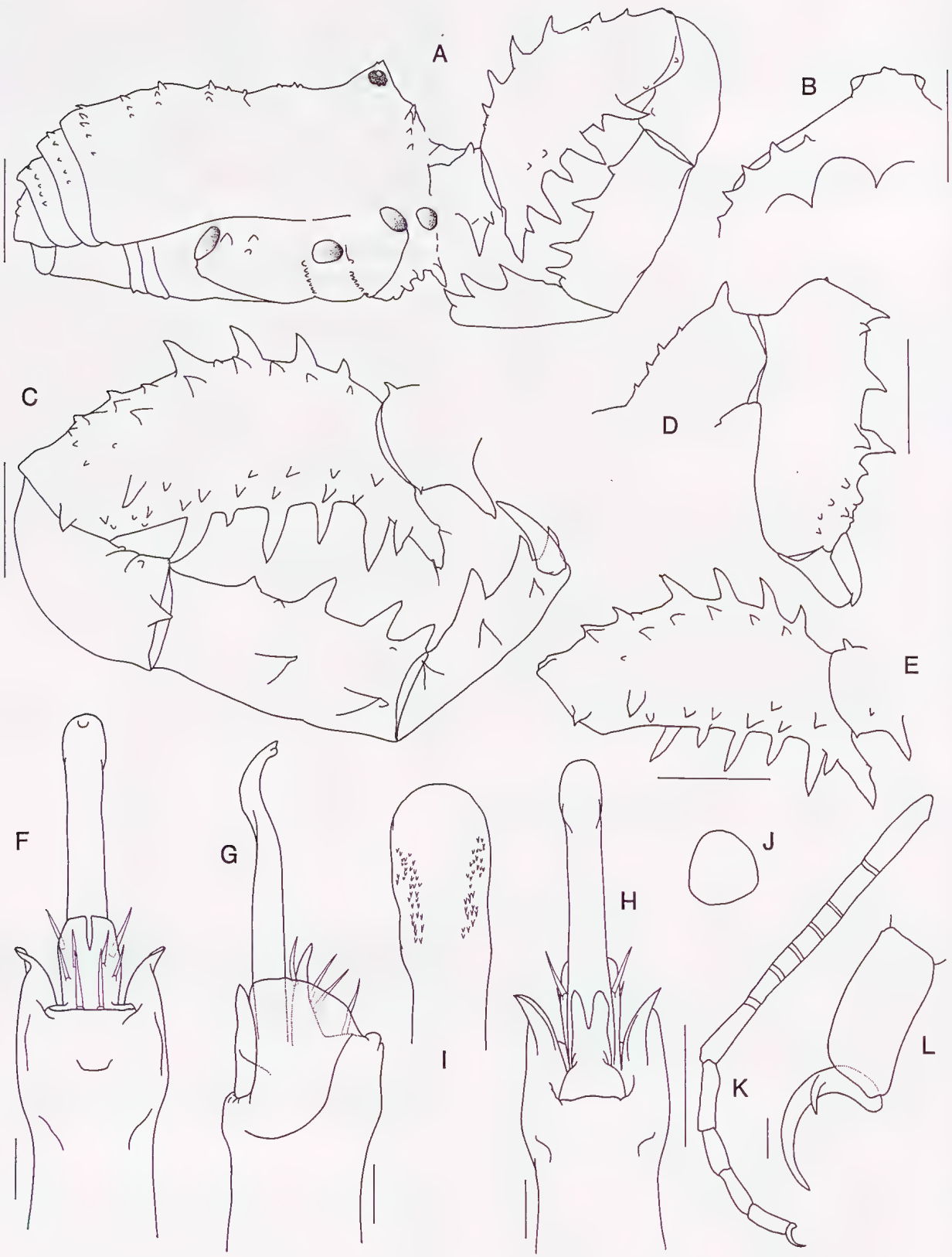

Fig.13. *Holonuncia recta* n.sp. E = female, KS21427, others = holotype male. A = body, lateral; B = eyemound and anterior spination, frontal; C = pedipalp except tarsus, prolateral; D = chelicera, retrolateral; E = pedipalp femur, prolateral; F-I = penis, F = ventral, G =lateral, H = dorsal, I = distodorsal part of stylus; J = genital operculum; K = metatarsus and tarsus of leg I, retrolateral; L = distal article of tarsus IV and claw. Scale bars: F-H = 0.1 mm, I = terminal part of H enlarged; L = 0.1 mm, others = 1.0 mm (J same scale as A).

2, FIV 3.81, FIV:CW 1.70; calcaneus I without notch, relatively long, CI:AI 0.36; lateral branch of tarsal claw IV inserted at about 0.5 claw length; tarsal formula 4(2),10-12(3),4,4. Ventral plate about as long as wide, median cleft about 0.5 plate length; in dorsal and ventral view glans somewhat narrow basally, broadens, constricts to a very narrow neck at about 0.7 glans length, termination similar to *H. seriata*.

FEMALE. Differs from male as in *H. cavernicola* except that body larger, CW 2.54-2.76(n=3), tubercles on anterior margin slightly more developed, distal accessory denticle present on trifid spine; calcaneus 1 without dimorphism; tarsal formula 3(2),11-14(3),4,4.

Variation. The size difference between the male specimen and three females may be due to sample size.

Comments. This species appears most closely related to *H. recta* which also lacks a notch in calcaneus I. I cannot determine whether specimens (females - SAM BS1731, BS1735) from nearby Indi Caves belong to this species, *H. recta*, or to a third species.

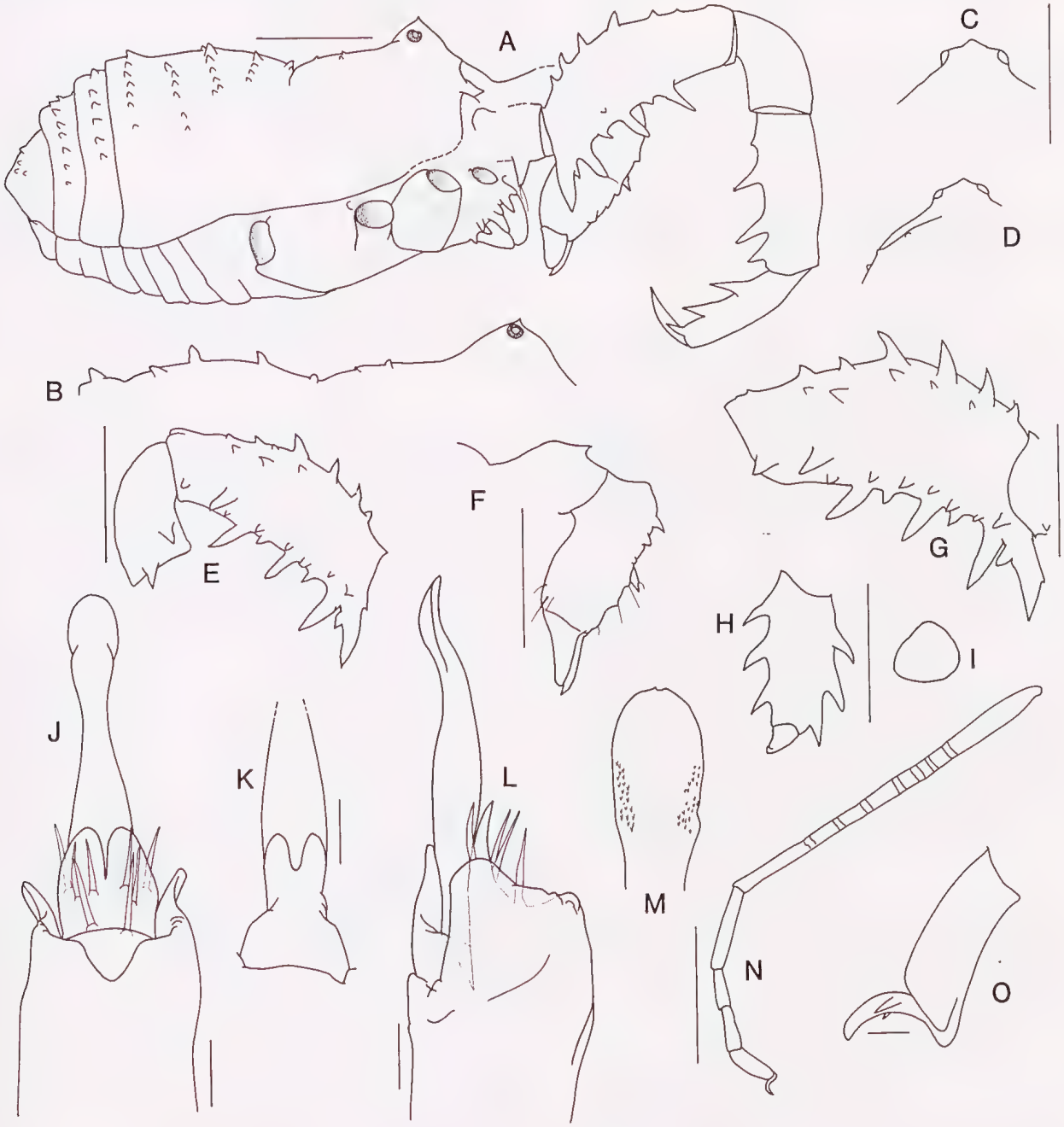

Fig.14. *Holonuncia hamiltonsmithi* n.sp. B,C,G = female, BS2205; others = holotype male. A = body, lateral; B = dorsal profile of scute; C-D = eyemound and anterior spination, frontal; E,G = pedipalp femur, prolateral; F = chelicera, retrolateral; H = pedipalp tarsus, ventral; I = genital operculum; J-M = penis, J = ventral, L =lateral, K = dorsal plate, M = distodorsal part of stylus; N = metatarsus and tarsus of leg I, retrolateral; O = distal article of tarsus IV and claw. Scale bars: J-L = 0.1 mm, M = terminal part of J enlarged; O = 0.1 mm, others = 1.0 mm (I same scale as A).

Etymology. The specific epithet acknowledges the contribution that Elery Hamilton-Smith has made to Australian biospeleology, including collection of the specimens for this species.

Distribution. Limestone Creek Caves in northern Victorian Alps.

Holonuncia kaputarensis n.sp.

Fig.15

Type material. New South Wales, Nandewar Ranges via Narrabri, 30°15'S 150°15'E. HOLOTYPE, male: Mount Kaputar National Park near Mount Kaputar turnoff, under log, field no. 2337, M.R. Gray and C. Horseman, 23 Feb. 1983.

Diagnosis. Notch in calcaneus I of male short and shallow, eyemound armed with spine, median cleft in penis ventral plate deep, greater than 0.5 plate length, distodorsal denticles on stylus large.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. CW 2.50 (n=1). Eyemound rising at about 70° from anterior margin, armed with a short spine, eyes not reduced; carapace lacking granules behind eyemound; TA1-5 slightly more tuberculate, mesial spine on TA1 larger than spine on TA2. CSL 1.87. PFL 2.13, PFL:CW 0.85; pedipalp femur with 5 mediodorsal spines size order 2=3,1,4,5 and 5 retroventral spines size order 1,3=4,2,5; retroventral spine 1 on tibia reduced to a denticle, tibia granulate ventrally. Calcaneus I short, CI:AI 0.15; notch very shallow. FIV 3.86, FIV:CW 1.54; tarsal formula 4(2),11(3),4,4. Width of ventral plate subequal to length, cleft deep, greater than 0.5 plate length and reaching almost to level of bases of distal pair of inferior setae; dorsolateral plate very broad, in lateral view obscuring mid-dorsal plate, in ventral view basal part broad and tapering abruptly to short lamina part; glans narrowest basally, broad apically; dorsal denticles larger, fewer and placed more terminally than in *H. cavernicola*.

Comments. Genital structure suggests a closer relationship to *H. enigma* than to other *Holonuncia* spp. *H. kaputarensis* is the most northerly record of the genus. The species is probably endemic to the Nandewar Ranges, an isolated 18.5 Ma volcanic mountain block which still retains moist habitat despite being surrounded by relatively dry alluvial plains. Two females of an undescribed *Holonuncia* sp. have been collected in the Warrumbungle Ranges, another isolated volcanic mountain block south-west of the Nandewars.

Etymology. The specific epithet refers to the type locality, Mount Kaputar.

Distribution. Mount Kaputar, and probably other moist regions of the Nandewar Ranges.

Holonuncia enigma n.sp.

Fig.16

Type material. New South Wales, northern suburbs of Sydney. HOLOTYPE, male: KS10577, Gordon, 33°52'S 151°12'E, pitfall trap in litter, field no. 2294, C. Horseman, 1 Jan. 1983. PARATYPES: KS13475, Gordon, pitfall trap in litter, C. Horseman, 1 Nov. 1983, 1 male; KS13323, same data, 12 Oct. 1983, 1 male; KS21445, Pymble area, G.S. Hunt, no date, 4 females; KS21446, St Ives, beside Ku-ring-gai Creek, under rotting wood, G.S. Hunt, 3 Aug. 1969, 1 male; KS19892, Lane Cove, Stringy Bark Creek, near Epping Road, under log, G.S. Hunt, Oct. 1988.

Diagnosis. Notch absent in calcaneus 1 of both sexes, retroventral spine 4 on pedipalp femur usually bifid, retrodistal spines 1 and 2 on pedipalp tarsus with thick bases, 3 segments in tarsus 1 and 6-7 in tarsus II of both sexes, dorsolateral plate of penis with lamina part visible only in dorsal view and not rising above level of the broad, finely denticulate basal part.

Description. MALE. This species differs in many respects from *H. cavernicola* (cave population): colour is yellow-orange with pigmentation pattern as figured; body small, CW 1.60 (n=1); eyemound rising at about 70° from anterior margin but sloping more gently posterior to eyes; eyes normal. Carapace lacking mesial granules posterior to eyes; mesial tubercles on TA3 not enlarged into spines; genital operculum width subequal to length. CSL 1.12, second segment of chelicera dorsally with large spines in distal half. PFL 1.35, PFL:CW 0.84; pedipalp femur with 7 mediodorsal spines size order 3=4=5,2,6=7,1 and 5 retroventral spines size order 4,1,3,2,5; spine 4 usually unevenly bifid; tibia granulate ventrally, retroventral spine 1 reduced to granule; retroventral spines 1 and 2 on tarsus thick at base. Legs short, FIV 1.52, FIV:CW 0.95; calcaneus I not notched below, CI:AI 0.18; tarsus IV dorsally with very large seta at about 0.4; tarsal formula 3(2),6-7(3),4,4. Ventral plate of penis about as wide as long, tendency for proximal pair of inferior setae to arise in a hollow is weak; dorsolateral plates broad and low, in lateral view obscuring base on mid-dorsal plate but not base of superior setae, basal part of plates enlarged and finely denticulate, lamina part of plate only visible in dorsal view and not rising above level of basal part; mid-dorsal plate cleft shallowly triangular; in ventral view glans narrowest basally, expanding gradually to about 0.66 and then expanding abruptly, in lateral view terminally bifurcate; distodorsal denticles larger and fewer than in *H. cavernicola*, similar in size to *H. kaputarensis*.

FEMALE. The female is very difficult to distinguish

from the male without lifting the genital operculum. There tend to be 4 subequal retrolateral spines on the tibia (3 in male), and spine 1 tends to be relatively larger. There is no dimorphism in tarsal segmentation, tarsal formula 3(2),6-7(3),4,4.

Variation. Accessory branch to retroventral spine 4 is sometimes lacking.

Comments. A monotypic genus was contemplated for this species but it is placed in *Holonuncia* on the basis of two synapomorphies: distodorsal denticles on the glans, and proximal inferior setae inserted in a hollow in ventral plate (though this is weakly

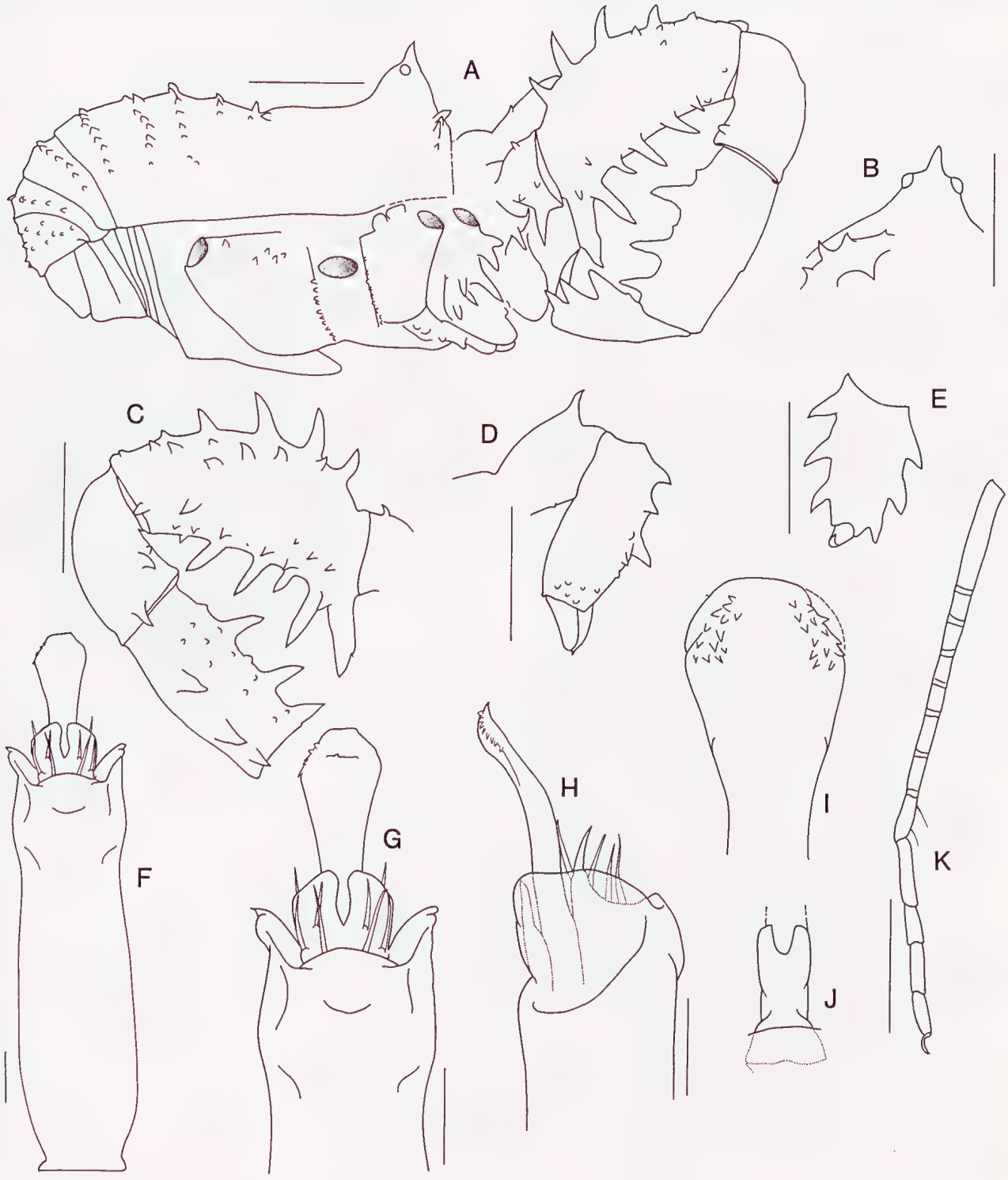

Fig.15. *Holonuncia kaputarensis* n.sp. Holotype male. A = body, lateral; B = eyemound and anterior spination, frontal; C = pedipalp except tarsus, prolateral; D = chelicera, retrolateral; E = pedipalp tarsus, ventral; F-I = penis, F = entire, G = ventral, H =lateral, J = dorsal plate, I = distodorsal part of stylus; J = genital operculum; K = metatarsus and tarsus of leg I, retrolateral. Scale bars: F-H,J = 0.1 mm, I = terminal part of G enlarged; others = 1.0 mm.

developed in this species). Generic placement will need to be revised should further, similar species be found.

Etymology. The specific epithet is a noun in apposition which underscores the peculiar nature of this species, particularly relating to aspects of genital morphology and the lack of sexual dimorphism in tarsus I segmentation.

Natural history. This species is probably more common in ground litter than its congeners.

Distribution. Northern suburbs of Sydney - valleys

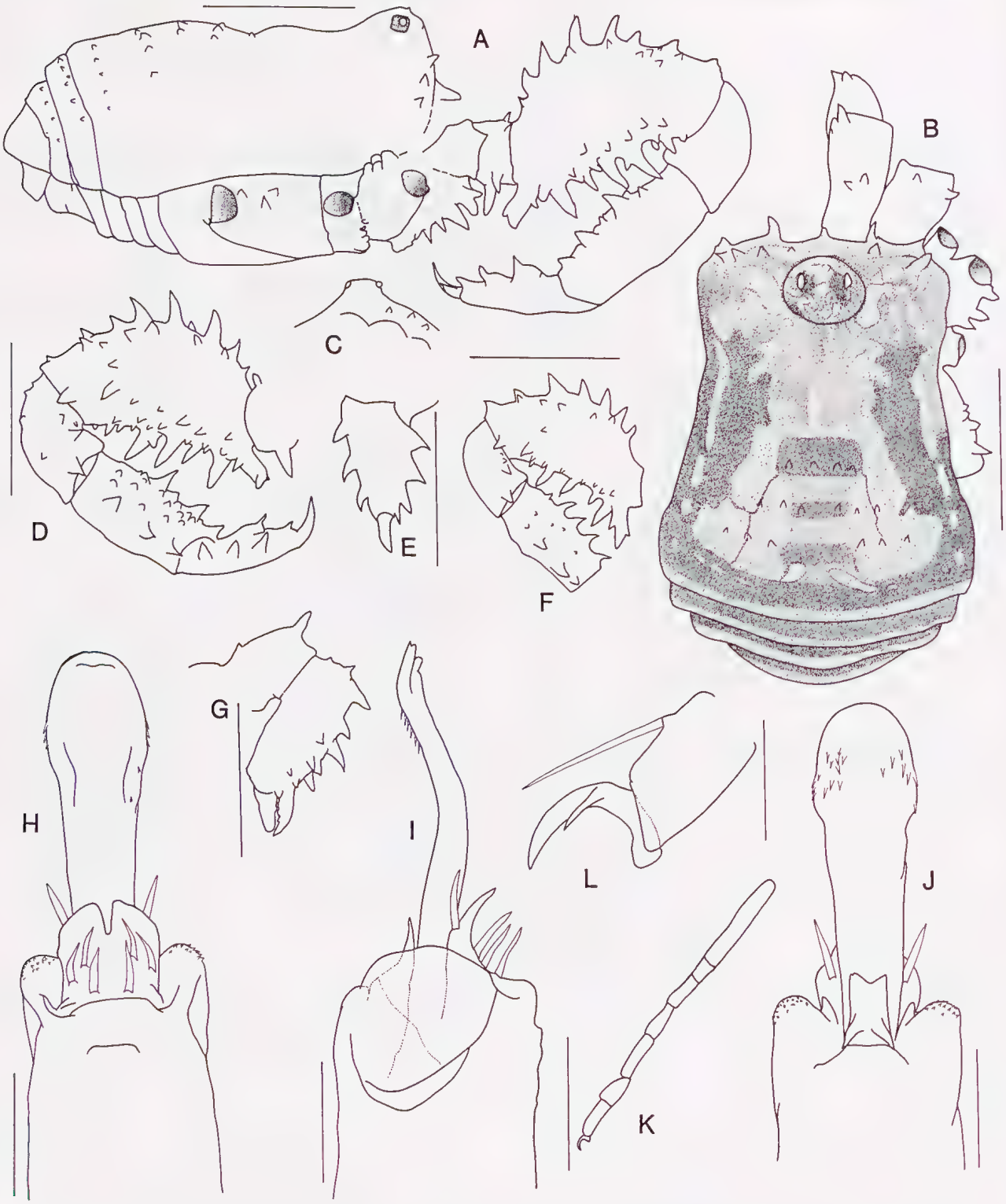

Fig.16. *Holonuncia enigma* n.sp. C,F = female, KS21445; others = male, KS10577. A = body, lateral; B = dorsum; C = eyemound and anterior spination, frontal; D = pedipalp, prolateral; E = pedipalp tarsus, ventral; F = pedipalp except tarsus, prolateral; G = chelicera, retrolateral; H-J = penis, H = ventral, J = dorsal I = lateral; K = metatarsus and tarsus of leg I, retrolateral; L = distal article of tarsus IV and claw with largest seta. Scale bars: H-J,L = 0.1 mm, others 1.0 mm.

in Hawkesbury Sandstone.

Other Cavernicolous Records

Holonuncia has been recorded from several other cave areas in New South Wales (Fig.1). Lack of males or doubts about identity have meant that some species descriptions have been deferred.

Three females have been collected in Timor (Isis River) Caves near Murrurundi, north of the Hunter River. They probably belong to a new species as other cavernicolous species occur south of the Hunter, a barrier implicated in the speciation of other harvestmen (Hunt, 1985). The females collected from Cliefden Caves, near Carcoar, have a canaliculate eyemound similar to that in *H. sussa*. These caves are distant from caves to the east (Fig.1), and so these specimens probably represent a new species. Similarly, the female specimens from the relatively isolated Abercrombie Caves may well belong to a new species. A sample lacking males has been collected from the Indi Caves in the Snowy Mountains on the New South Wales-Victorian border. The two males available from Wyanbene Cave near Braidwood have genitalia similar to *H. seriata* but, as the species occurs south of the Shoalhaven River, it may belong to a new species identified by electrophoresis (see below), or to a separate cavernicolous species.

Electrophoretic Study

A limited electrophoretic study was used to help resolve species boundary problems in *Holonuncia*. A study of the entire group was not practical so *H. seriata* and *H. francesae*, n.sp. were chosen. The latter possessed a short spine on the eyemound and four rather than five articles in tarsus I. However, the significance of these small differences was unclear in view of the seeming constancy of male genitalic characters. In addition, specimens from south of the Shoalhaven River (Sassafras and Tomerong) which had two morphologies resembling *H. francesae* and *H. seriata*, were chosen for comparison.

Methods and materials. Samples of *Holonuncia* spp. were collected at four sites: Ku-ring-gai Creek, St Ives; The Gib, Mittagong; Sassafras (between Nowra and Nerriga); and 3 km south of Tomerong. *Holonuncia* is closely related to *Equitius*, so samples from two nominal species, *E. doriae* (*ex* Mittagong) and *E. spinatus* (3 populations), were included for comparison. Specimens were held at -80°C until required. Variation at 20 enzyme loci (Table 1) was interpretable in a consistent Mendelian fashion. Electrophoretic methods for Titan III cellulose acetate plates and data analysis follow Colgan (1986), Richardson *et al.* (1986) and Ponder *et al.* (in press).

Results and discussion. Genetic distances are reported in Table 3 and summarised in Figure 17. A computer printout of allele frequencies for each population is available in the Australian Museum Library.

Although genetic distances are not final arbiters of specific status, the following conclusions are suggested by the data:

1. *H. francesae* n.sp. is a separate species from *H. seriata* (Roewer) despite the similarity in male genitalia. Fixed differences occur for AP-1, GPD, GOT-1, HK, TPI, and GPI. These differences contribute to a much greater genetic distance

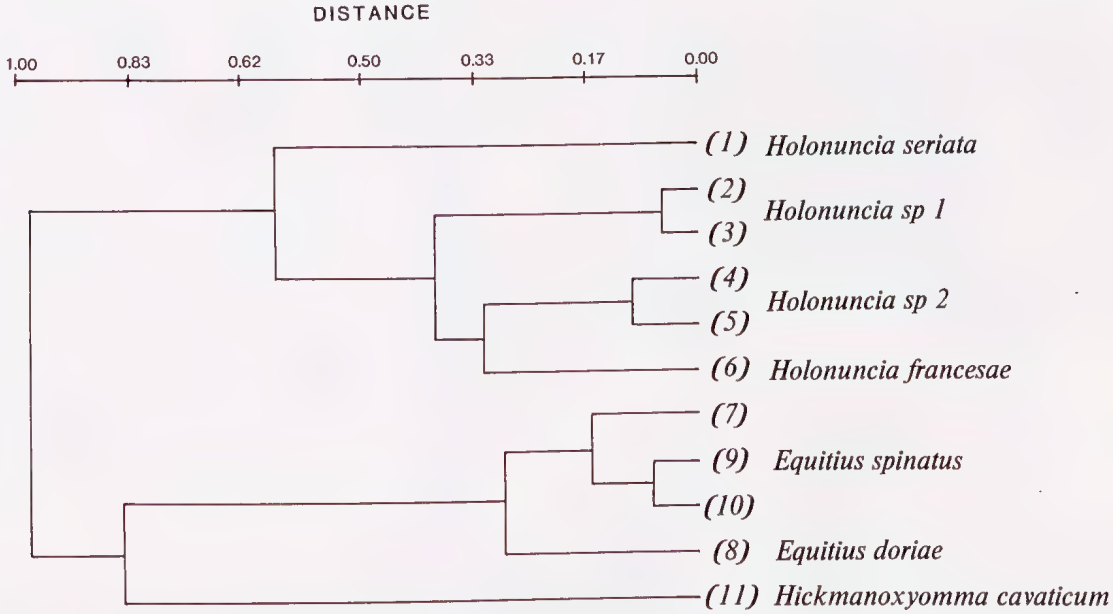

Fig.17. Distance tree based on genetic distances between selected populations of *Holonuncia*, *Equitius* and *Hickmanoxyomma*. Coefficient is Nei genetic distance. Numbers in parentheses refer to populations numbered in Table 2.

separating *H. francesae* n.sp. and *H. seriata* than that separating *E. doriae* and *E. spinatus* (Table 3; Fig.17).

2. *Holonuncia* sp.1 is morphologically very similar to *H. seriata* apart from having 4 articles in tarsus 1, but is genetically more similar to *H. francesae* (which also possesses 4 articles). In fact, this species was listed in "material examined" under *H. seriata* before electrophoretic analysis was undertaken. Material in the collection from Quiltys Mountain, Budawang Ranges, may belong to *Holonuncia* sp.1. Fixed differences between *Holonuncia* sp.1 and *H. seriata* occur for MDH-2, PGM, PK-2, TPI, FDP-1, and FDP-2. Again, the genetic distance between *H. seriata* and this new species is greater than that between the two *Equitius* spp.

3. *Holonuncia* sp.2 is sympatric with *Holonuncia* sp.1 near Tomerong (south of the Shoalhaven River) but is genetically more similar to *H. francesae* from the Sydney region (north of the Shoalhaven River) which it also resembles in carrying a small spine on the eyemound. Fixed differences between *H. francesae* and *Holonuncia* sp.2 occur for GPD, TPI, GPI and FDP-2. The distance between *H. francesae* and *Holonuncia* sp.2 is comparable to that between the two *Equitius* species. Fixed differences between the sympatric *Holonuncia* spp. 1 and 2 occur for GOT-2, PGM, PK-2 and TPI.

4. On the basis of the limited genetic distance data in this study, *Equitius* appears more closely related to *Hickmanoxyomma* than either is to *Holonuncia*, despite the fact that *Equitius* and most *Holonuncia* spp. possess a similar notch in calcaneus I.

Sample sizes of *Holonuncia* spp. 1 and 2 were small (Table 2). Description of these species will await the study of further material south of the Shoalhaven River to gauge both morphological and electrophoretic variation.

ACKNOWLEDGMENTS. This research was conducted with the assistance of an Australian Biological Resources Study grant. I also wish to thank the Directors of museums for making their collections available and the many speleologists for their essential efforts in collecting specimens from caves. Dr Dan Bickel and Dr Don Colgan have commented on the manuscript, while Ms Judy Thompson has helped with SEM work and specimen registration. Ms Grace Serkowski ran and scored the gels for electrophoresis, while Dr Don Colgan analysed the data. Mr Roger Springthorpe assisted with illustrations and Mr Gerard Clark with a computer program which assisted measurements.

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APPENDIX

Table 1. Enzymes scored in electrophoretic analyses.

Enzyme (E.C. Number)	Code	Alleles
Alkaline phosphatase (3.1.3.1)	AP-1	4
Malate dehydrogenase (1.1.1.37)	MDH-1	2
	MDH-2	3
Alanine aminotransferase (2.6.1.2)	GPT	1
Alpha-glycerophosphate dehydrogenase (1.1.1.8)	GPD	2
Fumerase (4.2.1.2)	FUM	3
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	GA3PDH	1
Aspartate aminotransferase (2.6.1.1)	GOT-1	4
	GOT-2	2
Phosphoglucomutase (2.7.5.1)	PGM	7
Hexokinase (2.7.1.1)	HK	2
Pyruvate kinase (2.7.1.40)	PK-2	2
6-phosphogluconate dehydrogenase (1.1.1.44)	6PGDH	4
Triosephophosphate isomerase (5.3.1.1)	TPI	3
Mannosephophosphate isomerase (5.3.1.8)	MPI	2
Glucosephophosphate isomerase (5.3.1.9)	GPI	5
Fructose diphosphatase (3.1.3.11)	FDP-1	3
	FDP-2	3
Isocitrate dehydrogenase (1.1.1.42)	IDH-1	3
	IDH-2	3

Table 2. Populations and sample sizes used for electrophoretic analysis.

Species	Population (No.)	Sample Size
Holonuncia seriata	The Gib, Mittagong (1)	3
Holonuncia sp. 1	Tomerong (2)	1
Holonuncia sp. 1	Tomerong (3)	1
Holonuncia sp. 2	Tomerong (4)	1
Holonuncia sp. 2	Sassafras (5)	1
H. francesae	St Ives (6)	4
Equitius spinatus	Johns River (7)	5
E. doriae	The Gib, Mittagong (8)	4
E. spinatus	Sandbar, Smiths Lake (9)	11
E. spinatus	The Grandis, Bullahdelah (10)	6
Hickmanoxyomma cavaticum	Mystery Creek Cave, Ida Bay (11)	2

Table 3. Genetic distances between *Holonuncia* spp., *Equitius* spp. and *Hickmanoxyomma cavaticum*. Nei Unbiased Genetic Distance above diagonal, Rogers Genetic Distance below. Numbers in parentheses refer to taxa numbered in Table 2.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
(1)	****	0.57	0.48	0.48	0.67	0.80	0.61	0.69	0.77	0.87	1.11
(2)	0.65	****	0.05	0.29	0.36	0.50	1.23	0.92	1.04	1.07	0.89
(3)	0.61	0.22	****	0.29	0.36	0.50	1.23	0.92	1.03	1.07	0.89
(4)	0.61	0.50	0.50	****	0.11	0.32	0.87	0.69	0.84	0.98	0.77
(5)	0.69	0.55	0.55	0.32	****	0.32	1.14	0.92	1.07	1.12	0.99
(6)	0.73	0.62	0.62	0.52	0.52	****	1.21	0.83	1.24	1.42	0.76
(7)	0.65	0.82	0.82	0.74	0.80	0.81	****	0.23	0.09	0.17	0.75
(8)	0.70	0.78	0.78	0.71	0.78	0.75	0.45	****	0.25	0.36	0.68
(9)	0.71	0.79	0.79	0.74	0.80	0.82	0.30	0.46	****	0.05	0.83
(10)	0.74	0.80	0.80	0.78	0.81	0.86	0.39	0.54	0.23	****	0.93
(11)	0.80	0.76	0.76	0.73	0.79	0.72	0.70	0.67	0.73	0.76	****

Records of the Australian Museum (1992) Vol.44: 165–183. ISSN 0067-1975

Salticidae (Arachnida: Araneae) from Oriental, Australian and Pacific Regions, VII. *Paraplatoides* and *Grayenulla* – New Genera from Australia and New Caledonia

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ABSTRACT. Genera *Grayenulla* from Australia and *Paraplatoides* from Australia and New Caledonia are diagnosed, described and illustrated. *Marptusa tenerrima* L. Koch, 1979 is established as the generic type of *Paraplatoides*. *Holoplatys caledonica* Berland, 1932 is included in *Paraplatoides*, as are four other new species: *P. longulus*, *P. hirsti*, *P. christopheri* and *P. nigrum*. Five new representatives of *Grayenulla* are described: *G. wishartorum*, *G. nova*, *G. dejongi*, *G. waldockae* and *G. australensis*.

ZABKA, M., 1992. Salticidae (Arachnida: Araneae) from oriental, Australian and Pacific Regions, VII. *Paraplatoides* and *Grayenulla* – new genera from Australia and New Caledonia. Records of the Australian Museum 44(2): 165–183.

Material and Methods

The paper is based on material from several collections listed below. Dimensions are given in millimetres. Details of terminology are presented for each genus separately. Format of leg spination follows Platnick & Shadab (1975). Dissected epigynes were digested in lactic acid for 10 to 30 minutes or in 10% KOH for 12 to 48 hours at room temperature, rinsed in distilled water and stained in ethanol solution of chlorazol black E under control and mounted in glycerin. The drawings were made using grid system.

Collections studied are as follows: AM – Australian Museum, Sydney; ANIC – Australian National Insect Collection CSIRO, Canberra; NMV – National Museum of Victoria, Melbourne; QM – Queensland Museum, Brisbane; SAM – South Australian Museum, Adelaide; TM – Tasmanian Museum and Art Gallery, Hobart; WAM – Western Australian Museum, Perth; ZMH – Zoologisches Institut und Zoologisches Museum, Universität Hamburg.

Abbreviations used are as follows: AEW – anterior eyes width, ag – accessory gland, AL – abdomen length, c – cymbium, CH – cephalothorax height, CL – cephalothorax length, co – copulatory openings, CW cephalothorax width, da – retrodorsal tibial apophysis, e – embolus, EFL – eye field length, ep – epigynal pocket, f – femur, fd – fertilisation duct, fp – femoral

process, id – insemination duct, m – metatarsus, P – prolateral spine, pt – patella, PEW – posterior eyes width, r – retrolateral spines, s – spermatheca, sc – scutum, sr – seminal reservoir, t – tibia, ta – retrolateral tibial apophysis, tg – tegulum, tf – tegular furrow, tr – trochanter, tp – tegular process.

Paraplatoides n.gen.

Type species. *Marptusa tenerrima* L. Koch, 1879 by original designation.

Etymology. The generic name is a random combination of letters and it is masculine in gender.

Diagnosis. The body flat and elongate. In some species similar to *Holoplatys*. Spines on first tibia always present, male palpal organ club-shaped, cymbium truncate at the top, embolus and insemination ducts long, the last coiled.

Description (Fig.1). Medium spiders, ranging from 4.30 to 7.20 mm in length. The body flat, narrow and elongate. Chelicerae of unident pattern, with 2 promarginal teeth and 1 retromarginal tooth. Legs I the strongest, *Holoplatys*-like, or more elongate, usually with prolateral (p) and retrolateral (r) spines on tibiae (t) and metatarsi (m). Legs IV longer than III. Genitalia almost identical in all species. Male palpal organ club-shaped, with tegular furrow (tf), embolus (e) long and thin, tibia (t) short and wide with single retrolateral

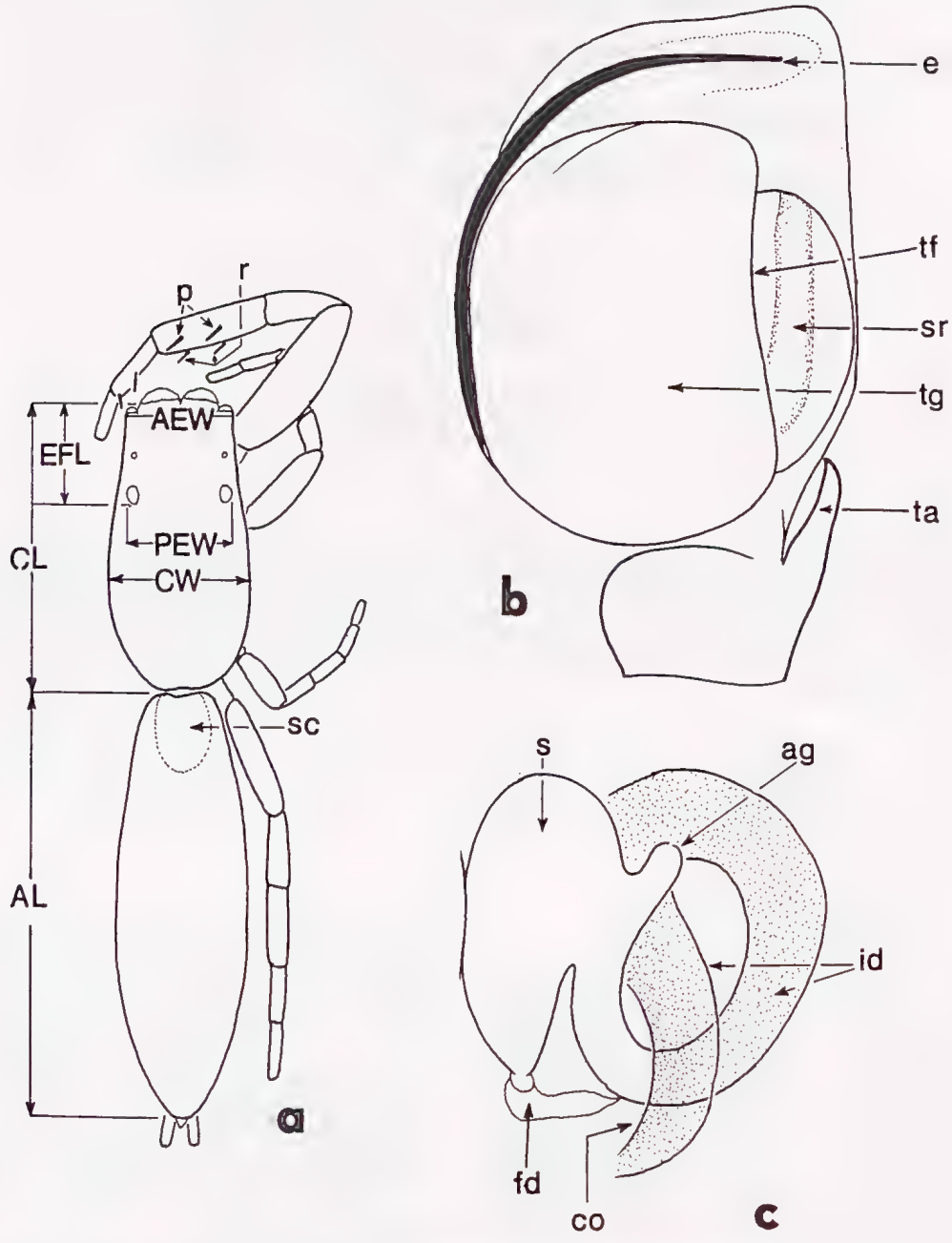
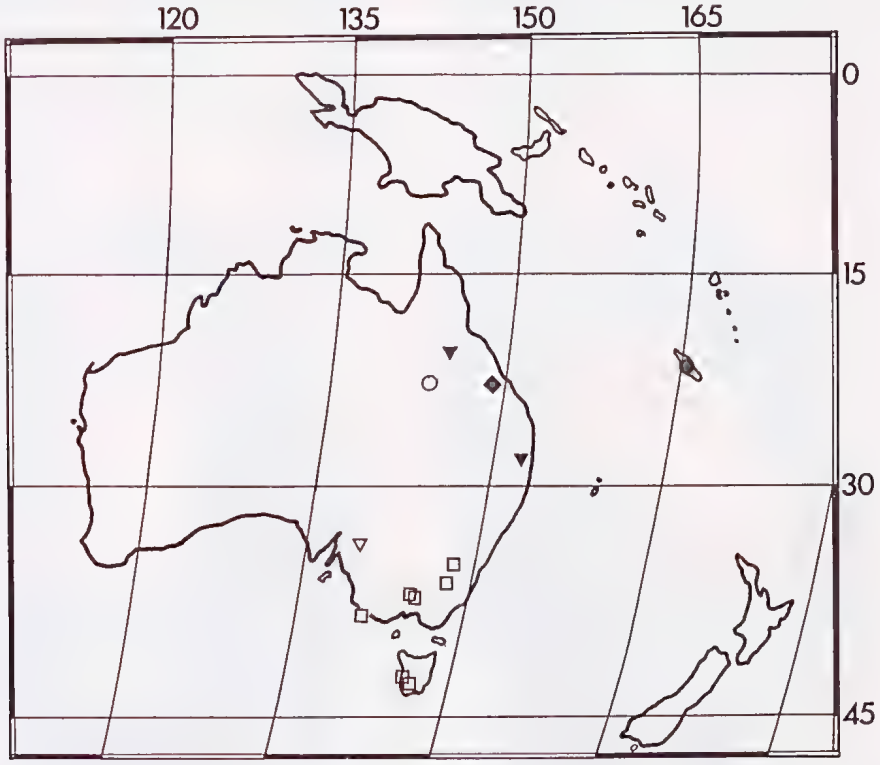


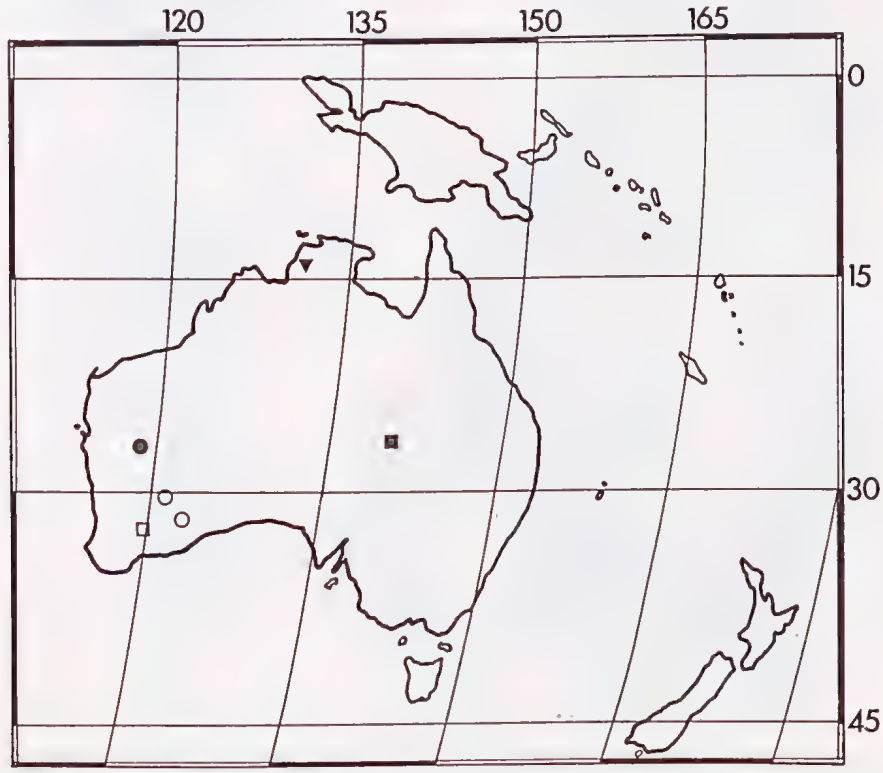
Fig.1. General characters of *Paraplatoides*: a – dorsal aspect, b – male palpal organ, c – female genitalia. (Abbreviations in the text).

apophysis (ta), sometimes with ventral process. Insemination ducts (id) long, with a single loop, their distal parts more sclerotised. Spermathecae (s) single-chambered, pear-shaped, accessory glands (ag) distinctive, fertilisation ducts (fd) oriented posteriorly.

Relationships. Genitalia and body form of most species show homologies with *Holoplatys* (Zabka, 1991a), *Ocrisiona* (Zabka, 1990) and some at present undescribed Australian genera. All represent one subfamily but because of the confused state of higher



Map 1. Distribution of *Paraplatoides*: closed circle – *P. caledonica* Berland; open circle – *P. longulus* n.sp.; closed inverted triangle – *P. christopheri* n.sp.; open inverted triangle – *P. hirsti* n.sp.; closed diamond – *P. tenerrima* (L.K.); square – *P. nigrum* n.sp.



Map 2. Distribution of *Grayenulla*: open circle – *G. australensis* n.sp.; closed circle – *G. waldockae* n.sp.; closed inverted triangle – *G. dejongi* n.sp.; closed square – *G. wishartorum* n.sp.; open square – *G. nova* n.sp.

taxonomy of the Salticidae it would be inadvisable to create any formal subfamily before revisions of the other genera involved are completed. The body structure and biology suggests that *P. nigrum* and *P. christopheri* are the closest relatives of *Holoplatys*. Other species seem more distant with *P. longulus* to be the most specialised in body form and leg armament. As in some other related genera (Zabka, 1991a), genitalia of particular species are very uniform in pattern, sometimes identical and as such almost useless as diagnostic characters. Other features are probably essential for interspecific separation. Unfortunately, except for the research of Jackson & Harding (1982) on the behaviour of some representatives of *Holoplatys*, there are no other studies dealing with the biology of this group of genera. *Paraplatoides tenerrima* (L. Koch, 1879) described as *Marptusa tenerrima,* and wrongly transferred to *Copocrossa* by Simon (1901), has been the only species of the genus known so far. *Copocrossa*, a genus of plurident

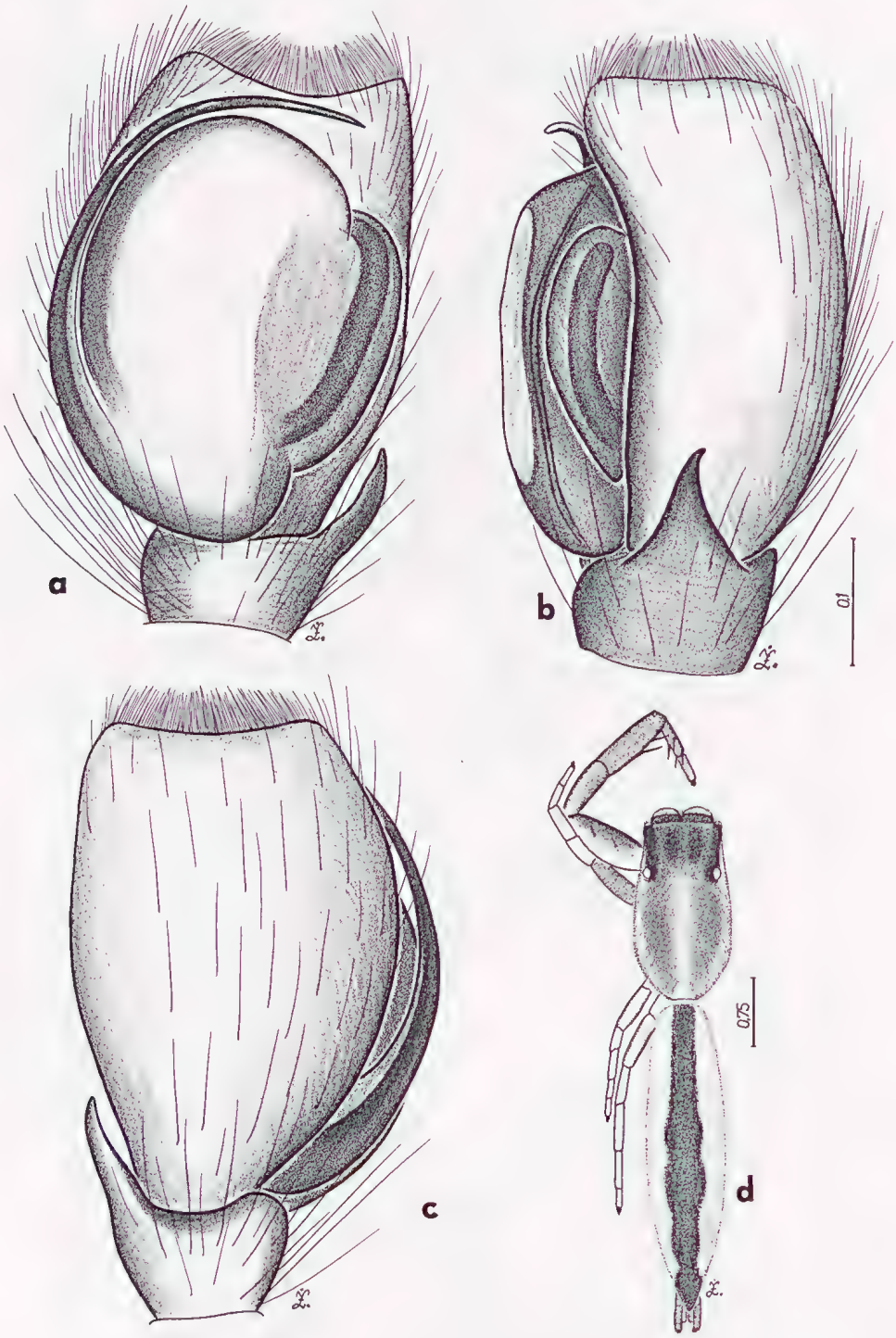


Fig.2. Male *Paraplatoides tenerrima* (L. Koch, 1879): ventral (a), retrolateral (b) and dorsal (c) aspects of palpal organ and general appearance of the holotype (d).

spiders with a completely different genitalic structure, represents a phylogenetically distant group (Davies & Zabka, 1989). Specimens of *Holoplatys caledonica* (Berl.) have not been located in any of main arachnological collections but the original description (Berland, 1932) gives sufficient information to allow the transfer of the species to *Paraplatoides*.

Biology and distribution. Little is know of the biology and distribution of species of *Paraplatoides*. Particular species have been collected under *Eucalyptus* bark or swept from vegetation, mostly from grass. The last have cryptic colour patterns, strongly elongated bodies and well-developed (oxyopid-like) spines on the first legs.

The genus appears to be widely distributed in Eastern Australia though most species are known only from single localities (Map 1). *Paraplatoides caledonica* (Berl.) is recorded from New Caledonia only.

Paraplatoides tenerrima (L. Koch, 1879) n.comb.

Fig.2, Map 1

Marptusa tenerrima L. Koch, 1879: 1115, n.syn.
Copocrossa tenerrima.–Simon, 1901: 475, n.syn.

Material examined. Queensland, HOLOTYPE, male, Peak Downs, (Mus. Godeffroy 16530), ZMH.

Diagnosis. Small, slender, long spider. Abdomen light with dark median stripe. First tibia and metatarsus

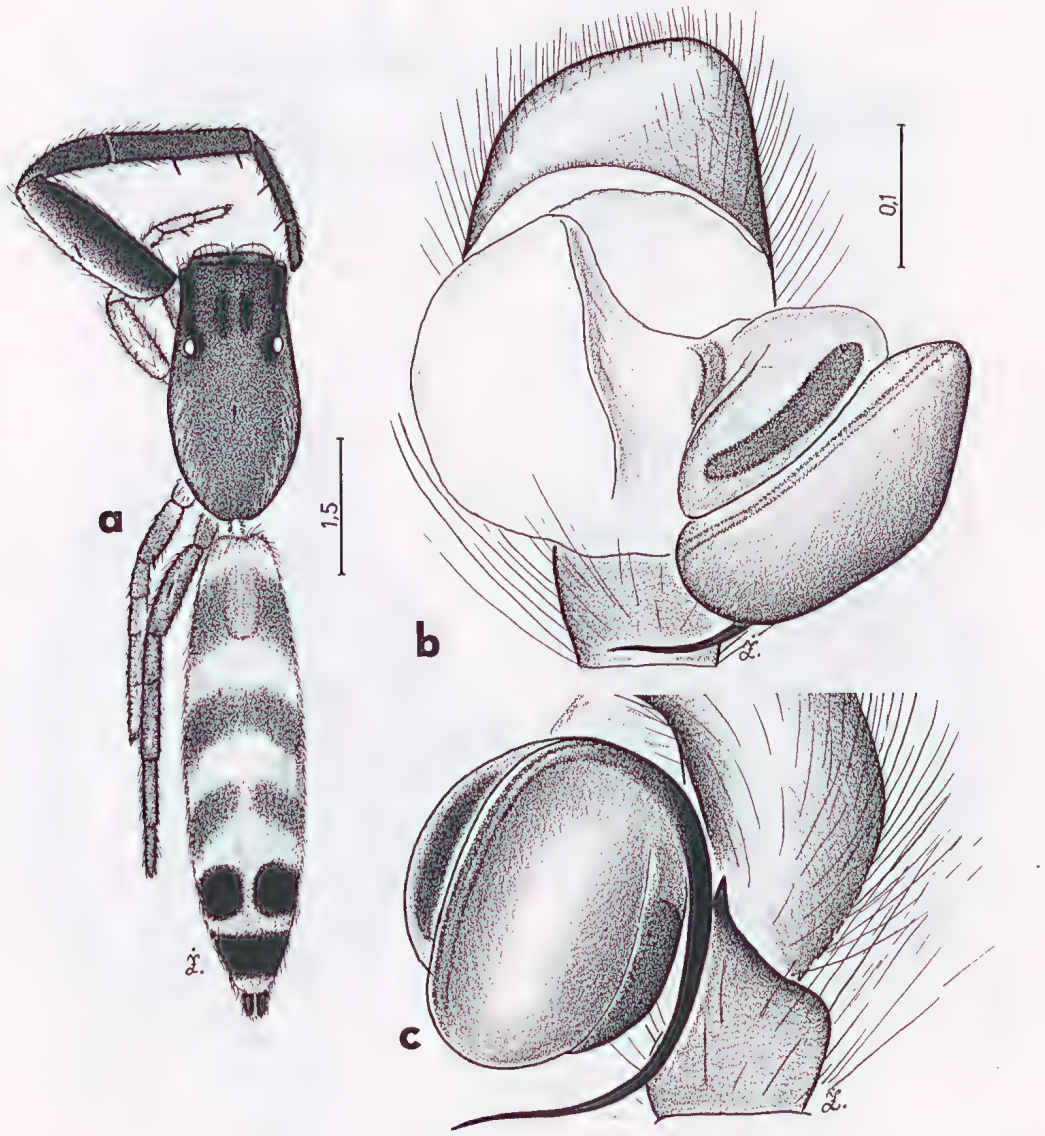


Fig.3. Male *Paraplatoides longulus* n.sp.: general appearance (a), ventral (b) and retrolateral (c) aspects of expanded palpal organ of the holotype.

with 2 pairs of long spines. In comparison to closely related *P. hirsti* abdominal scutum and spines on second metatarsi missing.

Male (Fig.2d). Cephalothorax dark-orange, darker around eyes, with 2 darker spots on eye field and lighter median and lateral stripes. Abdomen yellowish with dark median stripe. Spinnerets long and dark. Clypeus brownish, chelicerae brown, maxillae and labium lighter, with yellow tips. Sternum yellow, venter beige. Legs I orange-brown, strong. Other legs yellowish, their lateral surfaces darker.

Palpal organ as illustrated in Figure 2a-c.

Leg spination. tI: p1-1, r1-1, mI: p1-1, r1-1.

Dimensions. CL 1.65, CW 0.85, EFL 0.54, AEW 0.67, PEW 0.70, AL 2.70.

The female is unknown.

Paraplatoides longulus n.sp.

Fig.3, Map 1

Material examined. Queensland, HOLOTYPE, male, Mount Cameron. Winton, pitfall trap, 15-28 May 1977, A. Rozefelds, QM S3587.

Diagnosis. Abdomen very long with transverse zebra-like stripes and spots.

Male (Fig.3a). Cephalothorax dark-orange with darker eye surrounding and 2 dark spots on eye field. White hairs present marginally. Abdomen more elongate than in previous species, with transverse orange, black and beige stripes. Spinnerets black. Clypeus brown, chelicerae darker, maxillae and labium brown with lighter tips. Sternum orange, venter light-grey darkening posteriorly. Legs I longer than in *P. tenerrima* (L. K.), brown, dorsoventrally lighter. Other legs lighter, especially II and III.

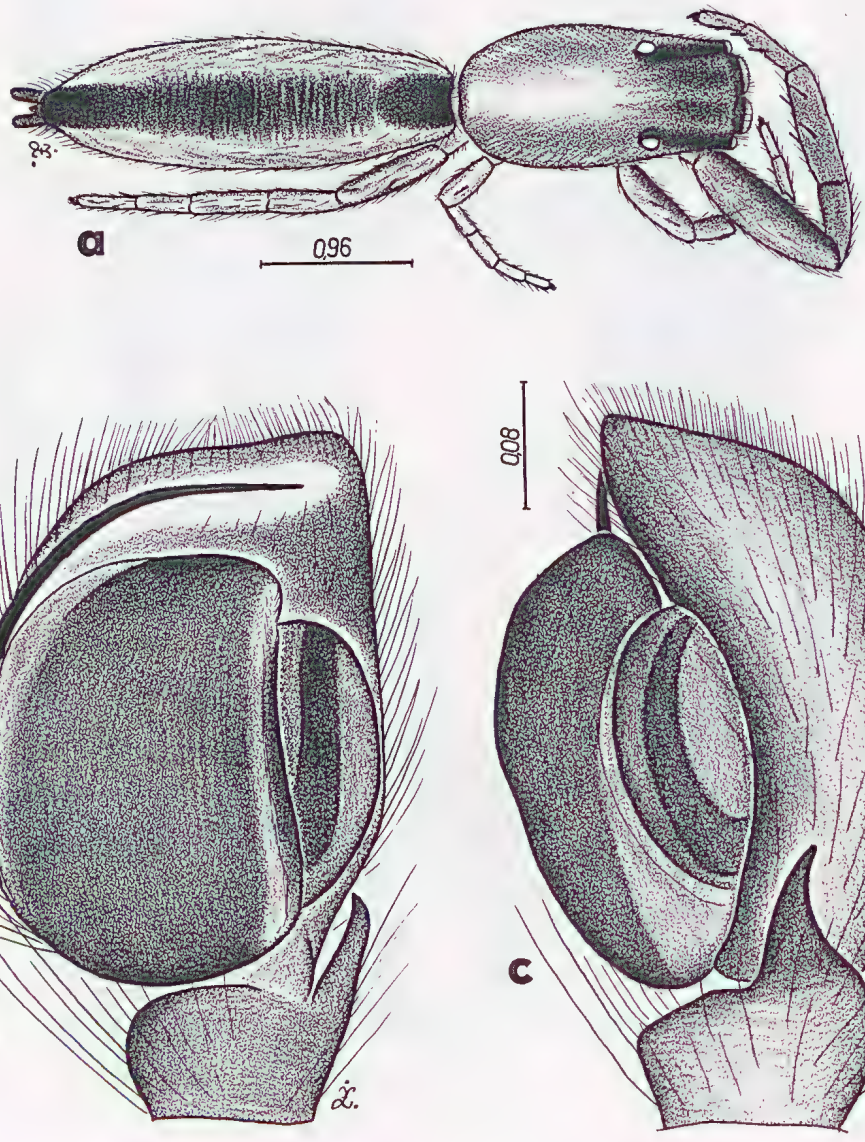


Fig.4. Male *Paraplatoides hirsti* n.sp.: general appearance (a), ventral (b) and retrolateral (c) aspects of palpal organ of the holotype.

Palpal organ (Fig.3b-c) expanded, difficult to compare with other species, but its general pattern as in type species.

Leg spination. tI: p1-1, r1-1; mI: p1-1, r1-1; mII: r1-0.

Dimensions. CL 1.90, CW 1.05, EFL 0.60, AEW 0.85. PEW 0.87, AL 3.45.

The female is unknown.

Paraplatoides hirsti n.sp.

Figs 4-5, Map 1

Material examined. South Australia, HOLOTYPE, male, 5 km south of Marcollat, 2 Feb. 1982, D. Hirst, SAM N1988358; ALLOTYPE, female, Morgan, 7 km north-west pipeline, Grass Tussock National Park, 18 Dec. 1976, P.J.M. Greenslade, SAM N1988359.

Etymology. The specific name is a patronym in honour of Mr David Hirst, collector of part of the material studied.

Diagnosis. In comparison to related *P. tenerrima*, anterior abdominal scutum and spines on second metatarsi are present.

Male (Fig.4a). Cephalothorax light-brown, lighter medially, dark around eyes, with 2 dark spots on eye field. Whole surface covered with white hairs.

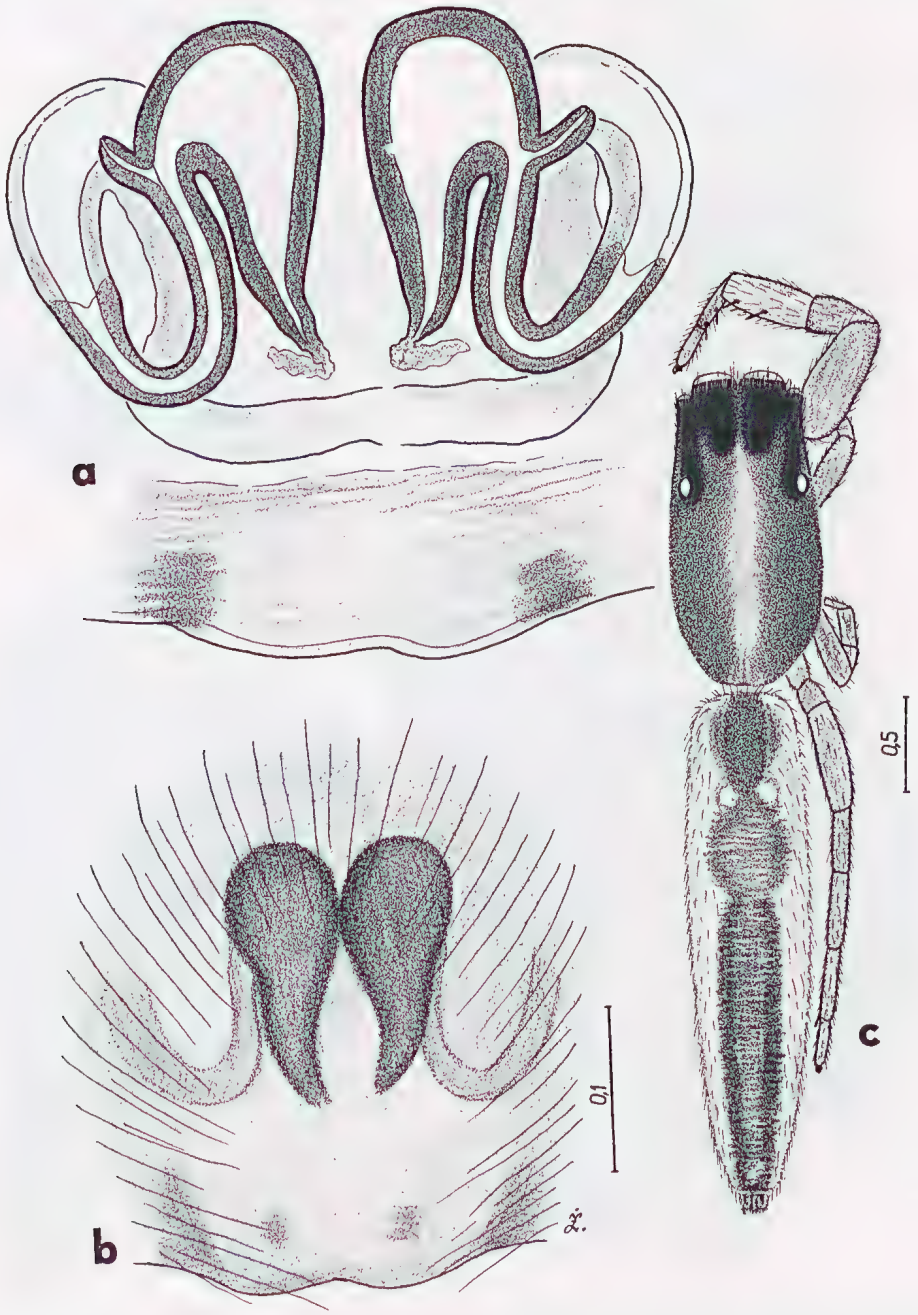


Fig.5. Female *Paraplatoides hirsti* n.sp.: internal genitalia (a), epigyne (b) and general appearance (c) of the allotype.

Abdomen beige with small anterior scutum and dark median stripe. Spinnerets dark. Clypeus dark, chelicerae dark-brown, maxillae and labium slightly lighter, sternum yellow with darker margin, venter beige. Legs I long, grey-brown. others orange, all legs darker laterally.

Palpal organ (Fig.4b-c) almost identical to other species, slightly less massive than in *P. tenerrima* (L. K.).

Leg spination. tI: p1-1, r1-1; mI: p1-1, r1-1; mII: r1-0.

Dimensions. CL 1.80, CW 1.00, EFL 0.58, AEW 0.75, PEW 0.78, AL 3.00.

Female (Fig.5c). Body form and colour pattern very similar to that in male, only legs lighter, yellow to orange, legs I shorter and more swollen than in male.

Genitalia (Fig.5a-b) with long insemination ducts, their proximal parts membranous, distal ones more sclerotised. Leg spination. tI: p1-1, r1-1; mI: p1-1, r1-1; mII: p1-0.

Dimensions. CL 1.65, CW 0.85, EFL 0.60, AEW 0.70, PEW 0.75, AL 2.85.

Paraplatoides christopheri n.sp.

Fig.6, Map 1

Material examined. Queensland, HOLOTYPE, male, Braemar State Forest, pitfall trap, Cypress and brigalow, 4-8 Feb. 1980, R. Raven, QM S3563; PARATYPE, male, Brisbane, Mount Coot-tha, dry *Eucalyptus* forest, sweeping grass, 21 Nov. 1987, M. Zabka, ZMH A87J89.

Etymology. The specific name is proposed in honour of my son Christopher (Krzysztof in Polish).

Diagnosis. Body almost black, abdomen with 2 transverse white spots in its posterior part. Spinnerets

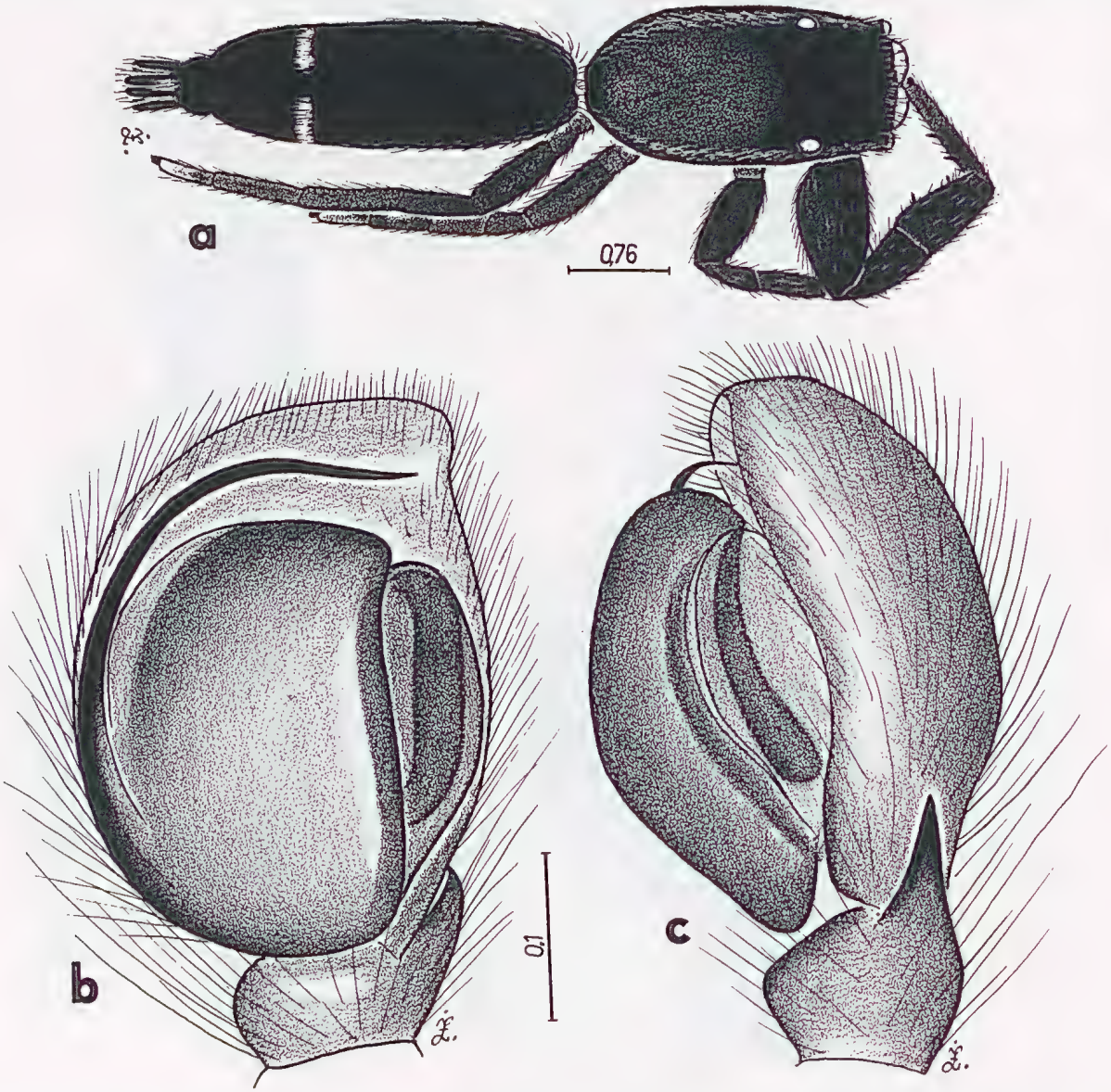


Fig.6. Male *Paraplatoides christopheri* n.sp.: general appearance (a), ventral (b) and retrolateral (c) aspects of palpal organ of the holotype.

particularly long.

Male (Fig.6a). Eye field black, thoracic part of cephalothorax slightly lighter. White hairs on lateral surfaces present. Abdomen black with white hairs marginally and with 2 transverse spots of white hairs in its posterior part. Spinnerets long, black clypeus and chelicerae dark-brown. Maxillae and labium dirty-brown, their tips lighter. Sternum dirty-brown, venter almost black. Legs generally dark, first ones almost black, massive, others slightly lighter.

Palpal organ (Fig.6b-c) as in other species of the genus.

Leg spination. tI: p1-1, r0-1; mI: p1-1, r1-1; mII: p0-1, r1-0.

Dimensions (holotype). CL 1.60, CW 1.00, EFL 0.55, AEW 0.77, PEW 0.81, AL 2.90.

The female is unknown.

Paraplatoides nigrum n.sp.

Figs 7-8, Map 1

Material examined. Tasmania, HOLOTYPE, male, Franklin River, 15 Jan. 1983, ANZES expedition, NMV; PARATYPES, 2 males, female, juvenile, Franklin, 8-9 June 1974, R. Mesibov, TM J995. Victoria, ALLOTYPE, female, Blackwood, Loam Creek, along Lerderberg Road, under ribbon bark, 10 Sept. 1977, ex Parnaby collection, AM

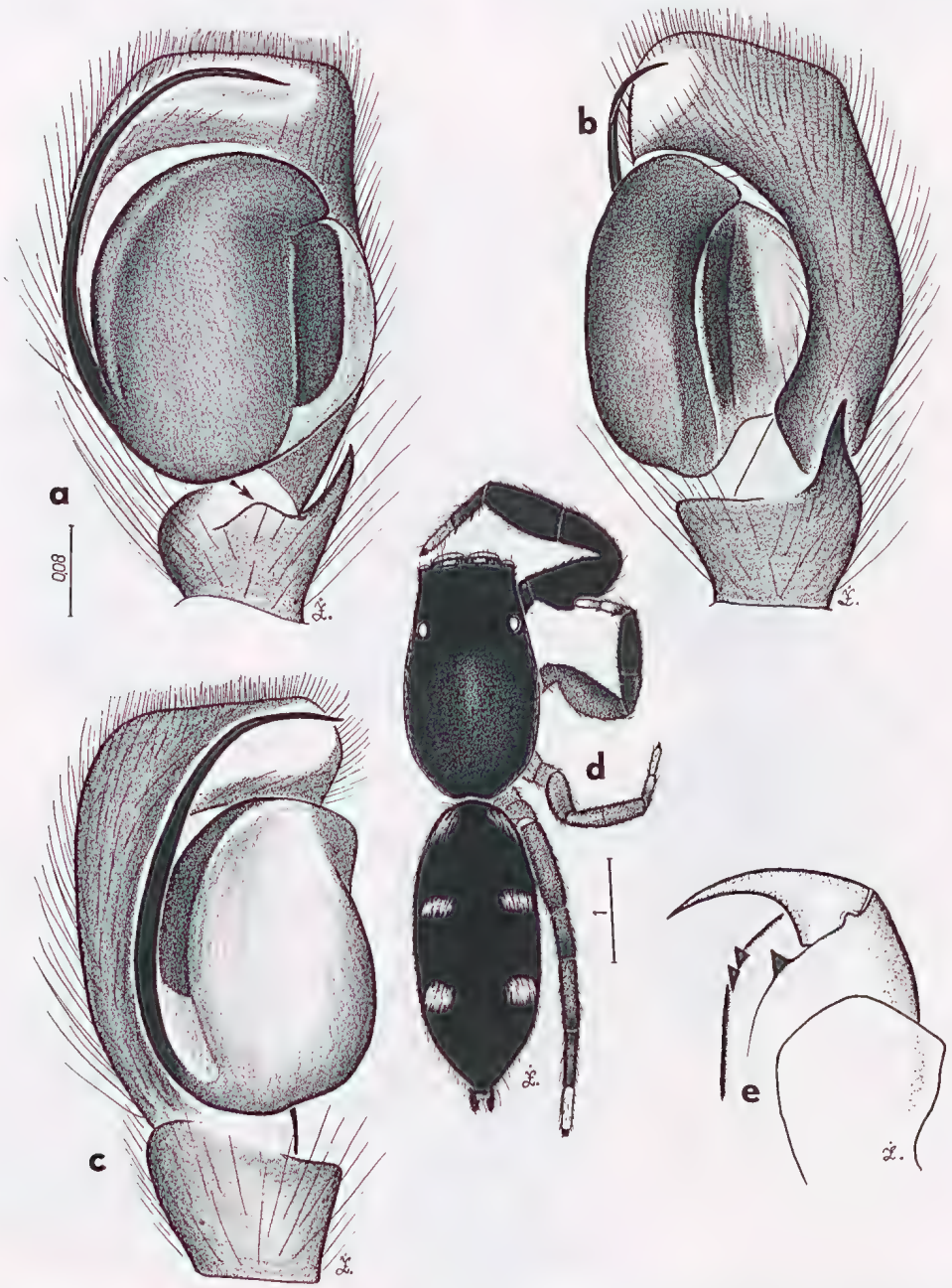


Fig.7. Male *Paraplatoides nigrum* n.sp.: ventral (a), retrolateral (b) and prolateral (c) aspects of palpal organ, general appearance (d) and cheliceral dentition (e) of the holotype. Ventral process on tibia marked with an arrow.

KS19287; PARATYPES, female, juvenile, Coranderrk Reserve, Healesville, under bark, 5 Mar. 1979, M.S. Harvey, WAM 89/274-5. New South Wales, PARATYPES, female, Brindabella Range, Moonlight Hollow, 2 km south-west of Bulls Head, Franklin Road, under bark of *Eucalyptus* sp. (gum bark), 3 Mar. 1983, M.S. Harvey, WAM 89/270; female, Kosciusko National Park, Tom Groggin, under bark of *Eucalyptus* sp., 12 May 1982, M.S. Harvey, WAM 89/271. South Australia, PARATYPE male, Ewen Ponds Reserve, pasture, under dead logs, 21 Apr. 1979, D. Lee, SAM N1988.

Diagnosis. Black spider, abdomen and spinnerets much shorter than in *P. christopheri*, the first with 3 pairs of white spots. Palpal organ with ventral tibial process (arrow).

Male (Fig.7d). Eye field black, thoracic part of cephalothorax brown with white hairs around lower margin. Abdomen almost black, with anterior scutum and 3 pairs of white tufts of hairs. Spinnerets black. Clypeus, chelicerae, maxillae and labium dark-brown, the last with lighter tips. Sternum orange to dirty-brown, darker marginally. Venter dark. Legs I black, only tarsi lighter. Other legs lighter distally and dorsoventrally.

Palpal organ (Fig.7a-c) with distinctive ventral process on tibia, in comparison to other species tegulum relatively smaller.

Leg spination. mI: p1-1, r1-1; mII: p1-1, r1-0.

Dimensions (holotype). CL 2.70, CW 1.75, EFL 0.75, AEW 1.10, PEW 1.10, AL 2.87.

Female (Fig.8a) coloured as male. Legs I shorter than those in male, dark-brown, other legs orange, darker

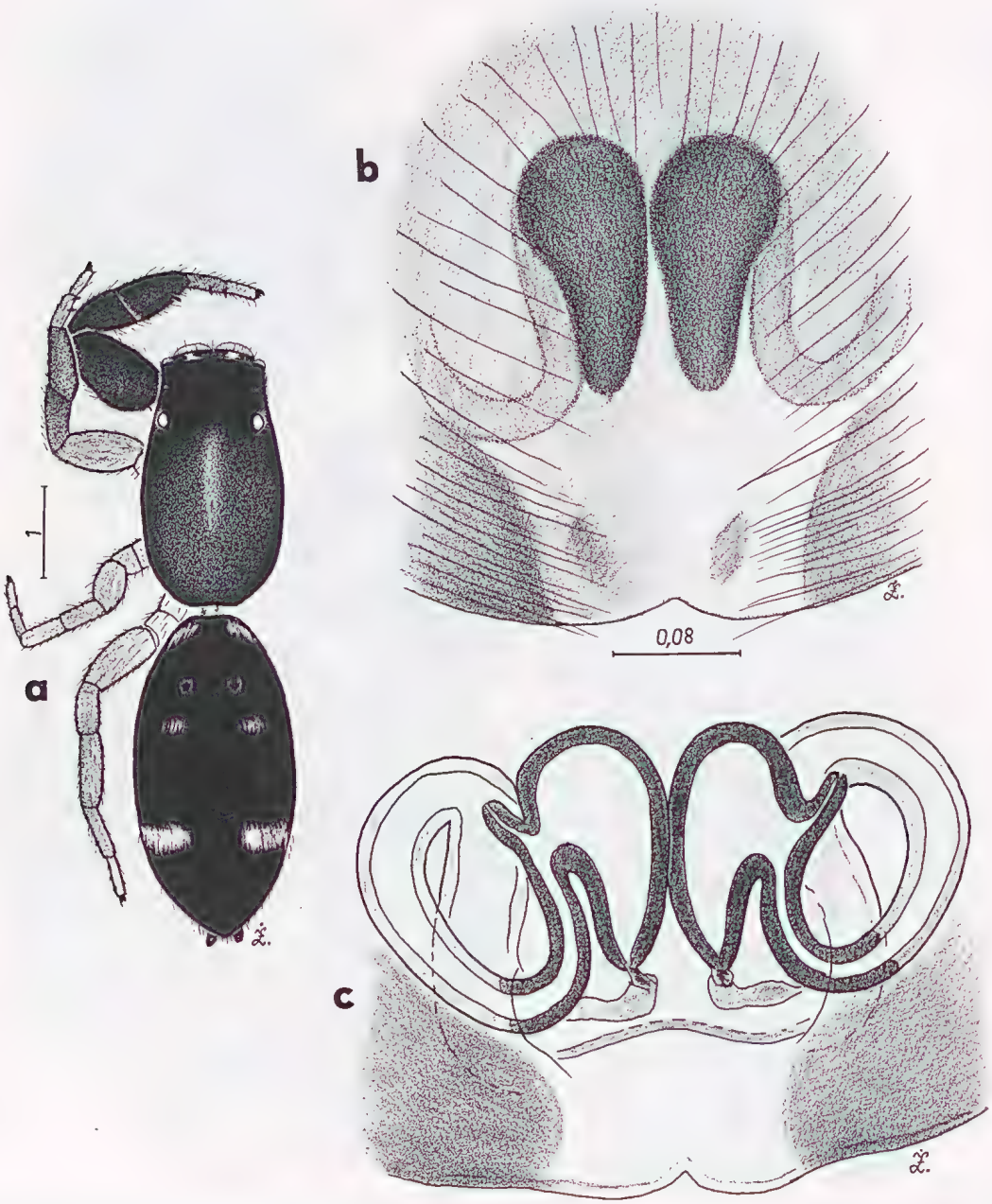


Fig.8. Female *Paraplatoides nigrum* n.sp.: general appearance (a), epigyne (b) and internal genitalia (c) of the paratype from Franklin.

around joints.

Genitalia (Fig.8b-c) similar to *P. hirsti*.

Leg spination. tI: p0-1; mI: p1-1, r1-1; mII: p1-1, r0-0 or r1-0.

Dimensions (allotype). CL 2.90, CW 1.75, EFL 0.80, AEW 1.20, PEW 1.20, AL 4.15.

Grayenulla n.gen.

Type species. *Grayenulla dejongi* n.sp. by original designation.

Etymology. The generic name is proposed in honour of Dr Michael R.B. Gray, arachnologist, Australian Museum, Sydney. The name is feminine in gender.

Diagnosis. The representatives of the genus can be recognised by body shape, 3 central bristles on clypeus and unique genitalic structure. Third legs distinctly the longest.

Description (Fig.9). Small to medium spiders, ranging from 2.55 to 4.50 mm in body length. Cephalothorax robust and high with distinctive cephalic and thoracic slopes. Abdomen oval, usually shorter than cephalothorax. Spinnerets normal. Clypeus with 3 protruding strong median bristles. Chelicerae vertical, with 1 fissident retrolateral tooth and a few teeth on prolateral margin. Legs III the longest, others more or less uniform in length. Male palps heavily haired. Between femur (f) and

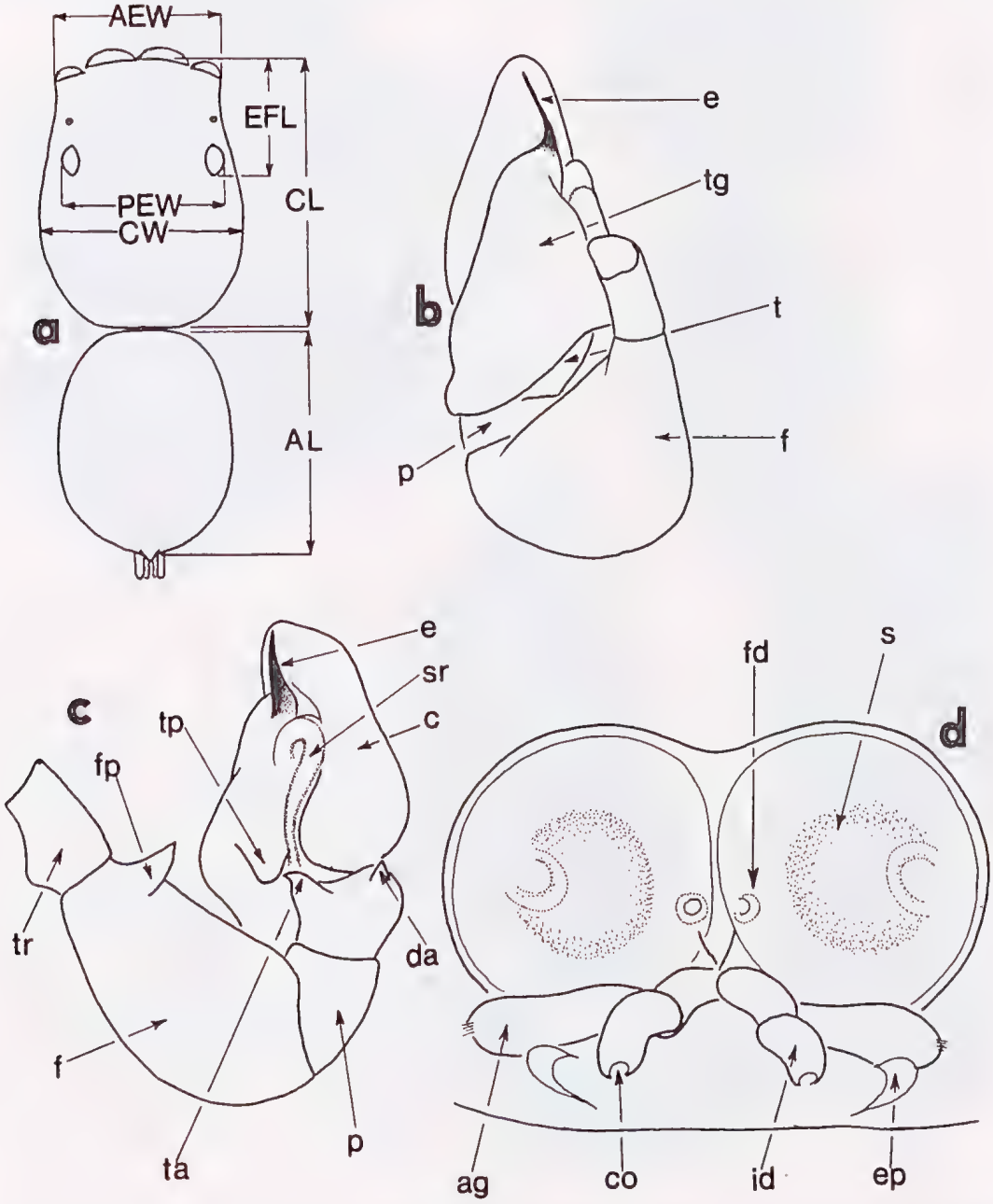


Fig.9. Morphological characters of *Grayenulla*: a – dorsal aspect, b-c – palpal organ, d – female genitalia. (Abbreviations in the text).

patella (pt) stable vertical connection, the first segment swollen with a triangular process (fp). Patella and tibia (t) with lateral brush of hairs, the last with retrolateral (ta) and retrodorsal (da) apophyses. Tegulum (tg) often triangular in shape, with process, embolus (e) straight or coiled distally. In one species cymbium laterally twisted. Seminal reservoir (sr) meandering. Epigyne with double pockets, accessory glands (ag) distinctive, insemination ducts (id) rather long, spermathecae (s) very large, spherical.

Relationships. *Grayenulla* is probably an endemic Australian genus that originated after Post-Gondwanan separation of the continent. It does not appear to be closely related to any other described salticid genus. There are some similarities in the structure of the genitalia with the South American genus *Hisucattus* (Galiano, 1985), the Asiatic *Synagelides* (e.g., Bohdanowicz, 1988) and the Australian genus *Pseudosynagelides* (Zabka, 1991b) but these are considered to be the result of convergence.

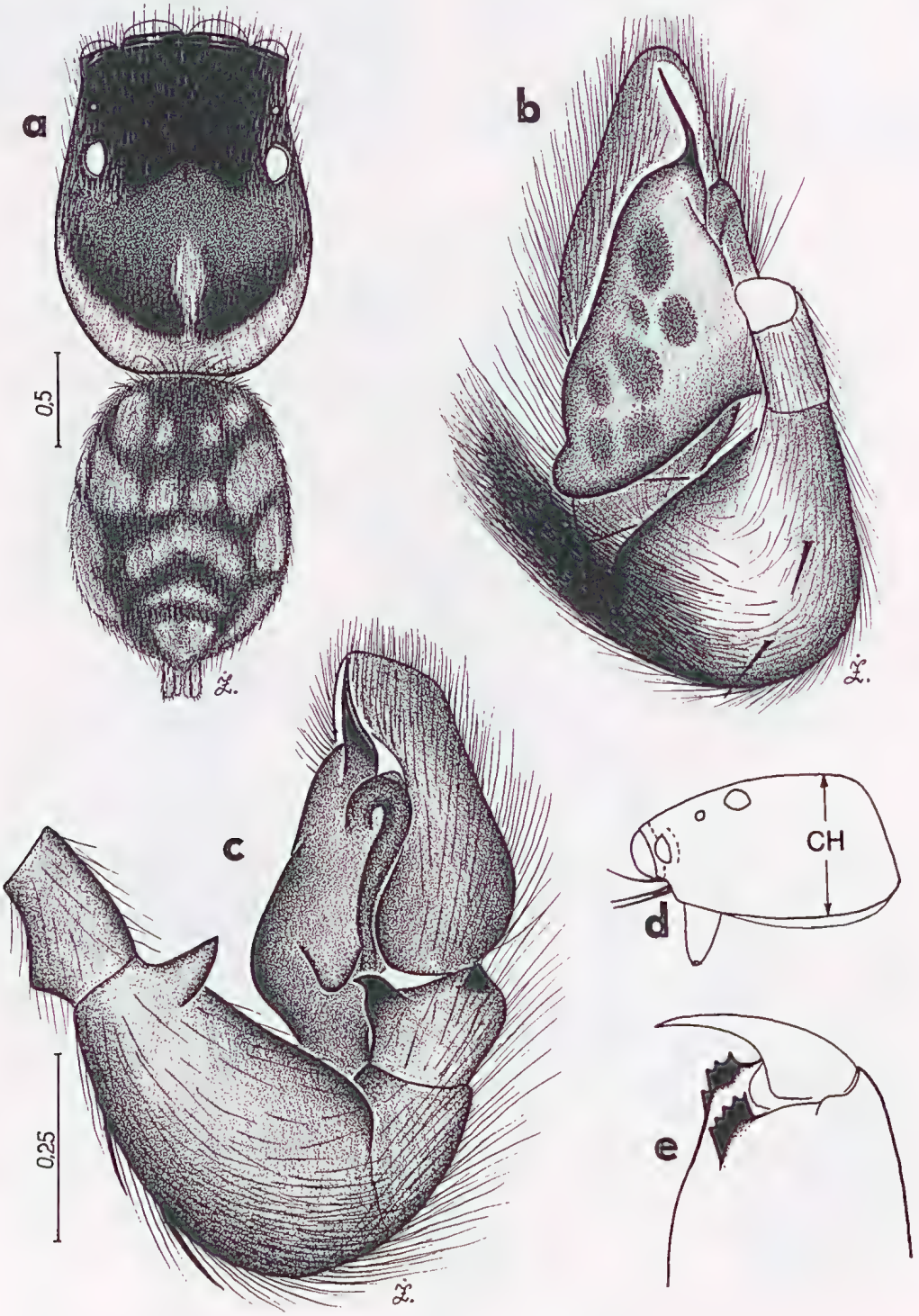


Fig.10. Male *Grayenulla dejongi* n.sp.: general appearance (a), ventral (b) and retrolateral (c) aspects of palpal organ, lateral view of cephalothorax (d) and cheliceral dentition (e) of the holotype.

Biology and distribution. All species are cryptic in colour and have been collected in dry, semidesert inland regions of Queensland and Western Australia, mostly by pitfall traps. No specimens have been found in the coastal part of the continent. Although there is little material available, the Australian interior seems to be a rich source of new, mostly endemic taxa (Zabka, unpublished).

Grayenulla dejongi n.sp.

Figs 10-11, Map 2

Material examined. Western Australia, HOLOTYPE, male, ALLOTYPE, female, PARATYPES, 2 males, female, 18 juveniles, Mitchell Plateau, Lone Dingo, pitfall traps, 9-19 May 1983, J. Cardale and I. Naumann, ANIC.

Etymology. The specific epithet is taken from the name of Mr Aris E. de Jong, Western Australian naturalist.

Diagnosis. Femora of the first legs in males metallic-black, palpal femora with prolateral brush of hairs, tegulum almost triangular, embolus pointed. Insemination ducts long and coiled.

Male (Fig.10a). Eye field dark-brown, thorax dirty-brown, with marginal belt of white hairs. Abdomen dark-grey with large light spots. Spinnerets dirty-beige. Clypeus light-brown with single hairs and 3 strong bristles (Fig.10d). Chelicerae (Fig.10e) orange, maxillae and labium orange with yellow

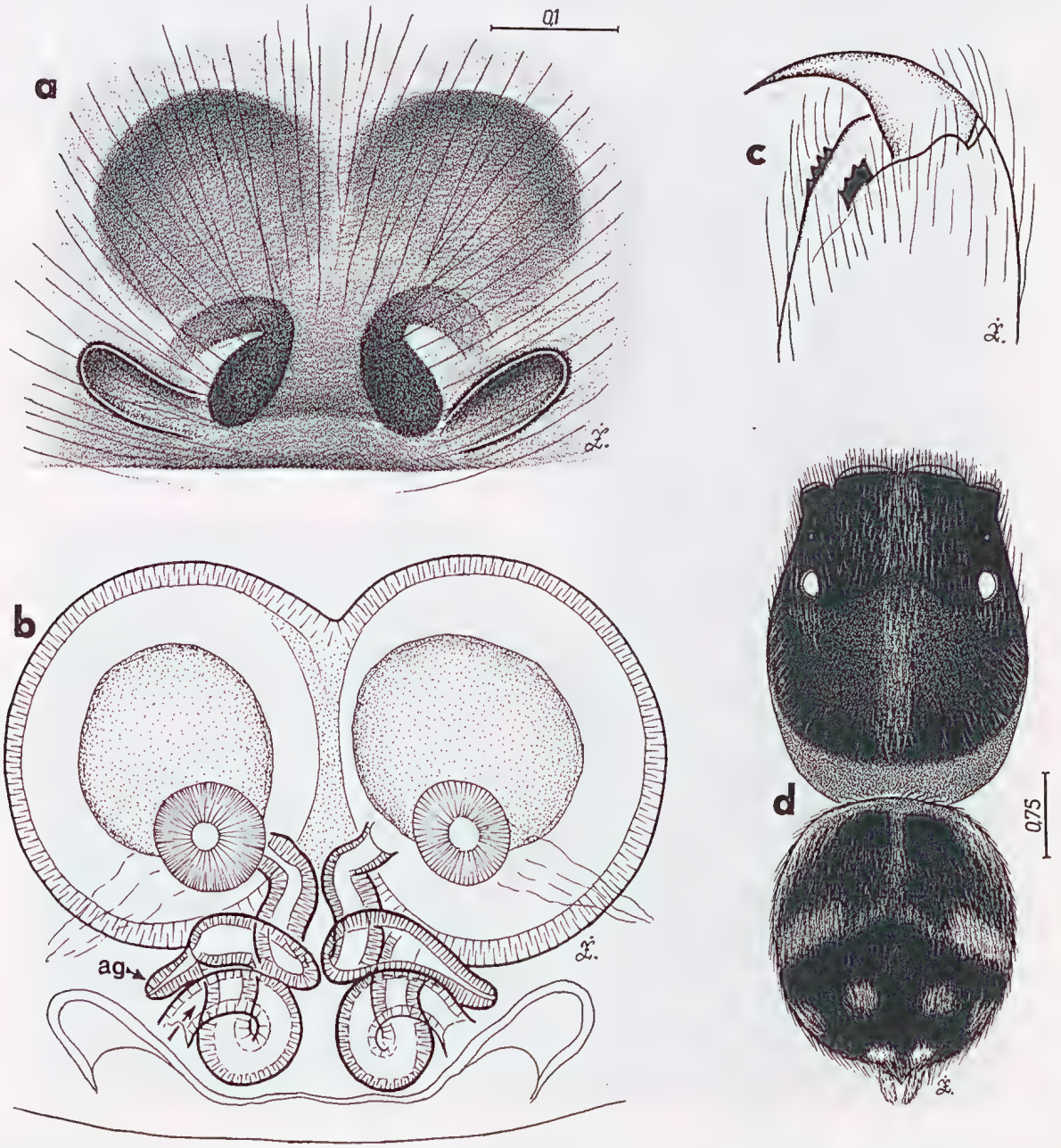


Fig.11. Female *Grayenulla dejongi* n.sp.: epigyne (a) and internal genitalia (b), cheliceral dentition (c) and general appearance (d) of the allotype.

tips, sternum and venter yellowish. Prolateral femora of legs I metallic black, also other segments dark. Legs IV beige, lighter ventrally, darker around joints.

Palpal organ (Fig.10b-c) with triangular, dark spotted tegulum. Retrolateral tibial apophysis hook-like, retrodorsal apophysis small, conical.

Dimensions (holotype). CL 1.80, CW 1.40. CH 0.95, EFL 0.71, AEW 1.15. PEW 1.05, AL 1.45.

Female (Fig. 11d) similar in colour to the male, but more robust and haired. All legs almost uniform in colour, beige, darker around joints. Chelicerae (Fig.11c) coloured as in male.

Epigyne and internal genitalia as illustrated in Figure 11a-b. Insemination ducts coiled, longer than in *G. nova*.

Dimensions (allotype). CL 2.40, CW 1.95, CH 1.33, EFL 0.80, AEW 1.48, PEW 1.48, AL 2.30.

Grayenulla wishartorum n.sp.

Figs 12-13, Map 2

Material examined. Queensland, HOLOTYPE, male. PARATYPES, 2 males, Birdsville, L. Muncoonie, desert, pitfall trap, 12-17 Nov. 1976, R. Raven, A. Berg, QM S4772.

Etymology. The specific epithet is proposed in honour of my Australian friends, amateur arachnologist Mr Graham Wishart and his wife Gwenneth.

Diagnosis. Embolus long, twisted distally, chelicerae with prolateral fringe.

Male (Fig.12a). Cephalothorax dark-brown with numerous white hairs. Abdomen beige with large lighter spots, its anterior part darker medially. Spinnerets beige. Clypeus light-brown, fringed with numerous white hairs. Chelicerae (Fig.12b) with fringe

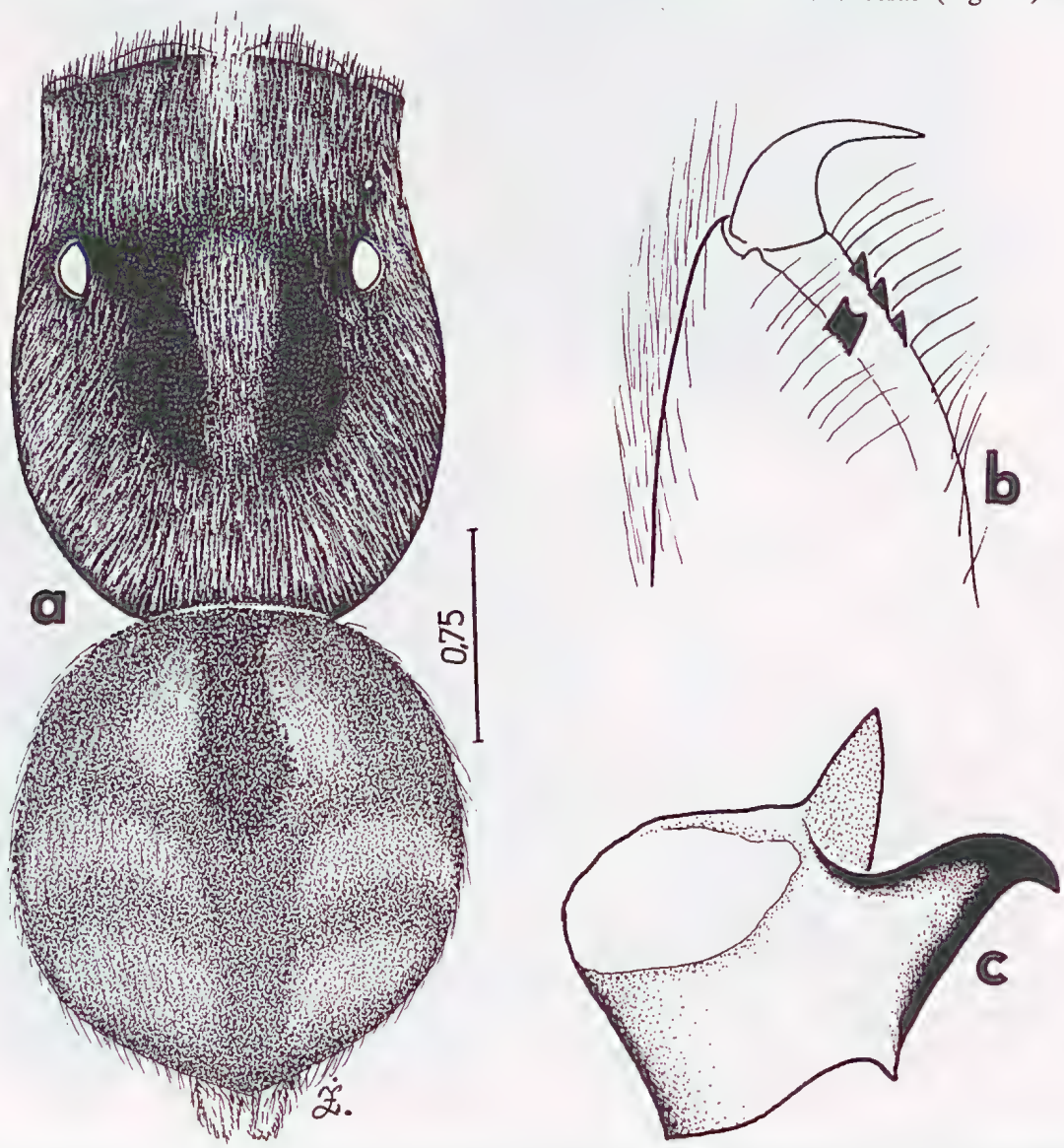


Fig.12. Male *Grayenulla wishartorum* n.sp.: general appearance (a), cheliceral dentition (b) and palpal tibia (c) of the holotype.

of long white hairs on prolateral surface. Maxillae and labium honey-yellow with lighter tips. Sternum dirty-brown, covered with numerous white hairs. Venter beige. Legs yellowish with darker joint area, tarsi with dark hairs, especially on first and second legs.

Palpal organ (Figs 12c, 13a-d) more specialised than in other species; cymbium laterally twisted, embolus long and coiled distally.

Dimensions. CL 1.90, CW 1.49, CH 0.98, EFL 0.88, AEW 1.34, PEW 1.28, AL 1.67.

The female is unknown.

***Grayenulla waldockae* n.sp.**

Fig.14, Map 2

Material examined. Western Australia, HOLOTYPE, male, PARATYPES, 2 males, 2 juveniles, Woodstock Station, site WS5, wet pitfall traps, May 1988, J.M. Waldock, WAM 88/2156-60.

Etymology. The specific epithet is proposed in honour of Miss Julianne M. Waldock, arachnologist, Western Australian Museum, Perth, collector of the material studied.

Diagnosis. Femur strongly swollen, tegulum oval,

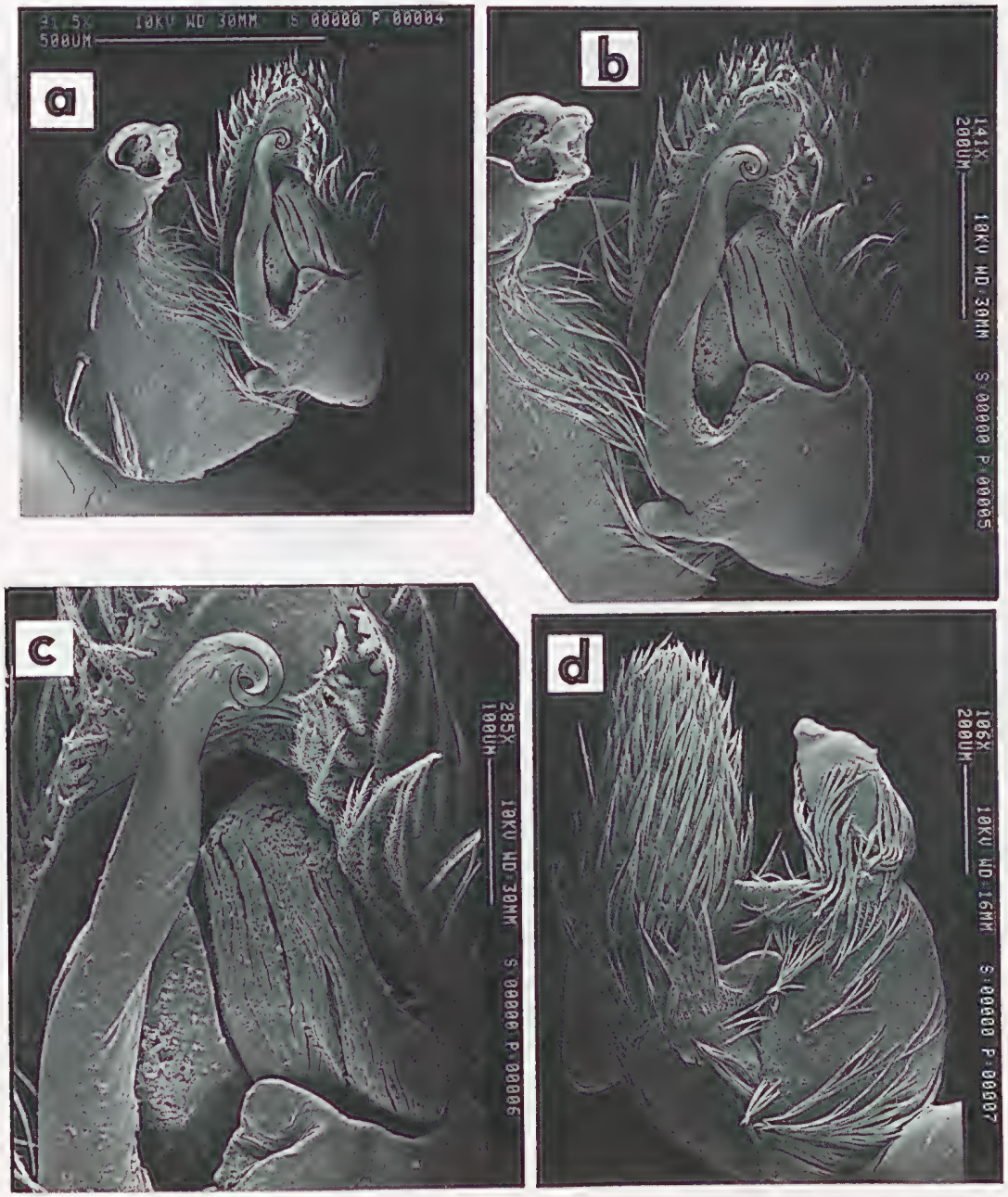


Fig.13. Male *Grayenulla wishartorum* n.sp.: ventral (a-c) and prolateral (d) aspects of palpal organ of holotype.

seminal reservoir distinctive, embolus thick.

Male (Fig.14a,c). Eye field grey-brown, thorax orange. Abdomen beige with darker anterior median stripe. Spinnerets beige. Clypeus dirty, with orange and grey hairs and with central fringe. Chelicerae (Fig.14b) dirty-brown, their tips orange. Maxillae and labium yellow to honey-orange, sternum and venter yellow to beige. Legs yellow to beige, slightly lighter distally tarsal tips contrasting black.

Palpal organ as illustrated in Figure 14d-f.

Dimensions (holotype). CL 1.46, CW 1.17, CH 0.72, EFL 0.56, AEW 0.99, PEW 0.98, AL 1.21.

The female is unknown.

Grayenulla australensis n.sp.

Fig.15, Map 2

Material examined. Western Australia, HOLOTYPE, male, Woodline, WAM Goldfield Survey, *Eucalyptus dundasii* woodland, pitfall traps, 7-12 Mar. 1980, W.F. Humphreys *et al.*, WAM 88/2161; PARATYPE, male, Goongarrie, dune, pitfall traps, 6-11 Oct. 1980, W.F. Humphreys *et al.*, WAM 88/2142.

Diagnosis. Palpal organ similar to *G. waldockae* but femur less swollen, tegulum more irregular in shape, without spots and embolus pointed. In

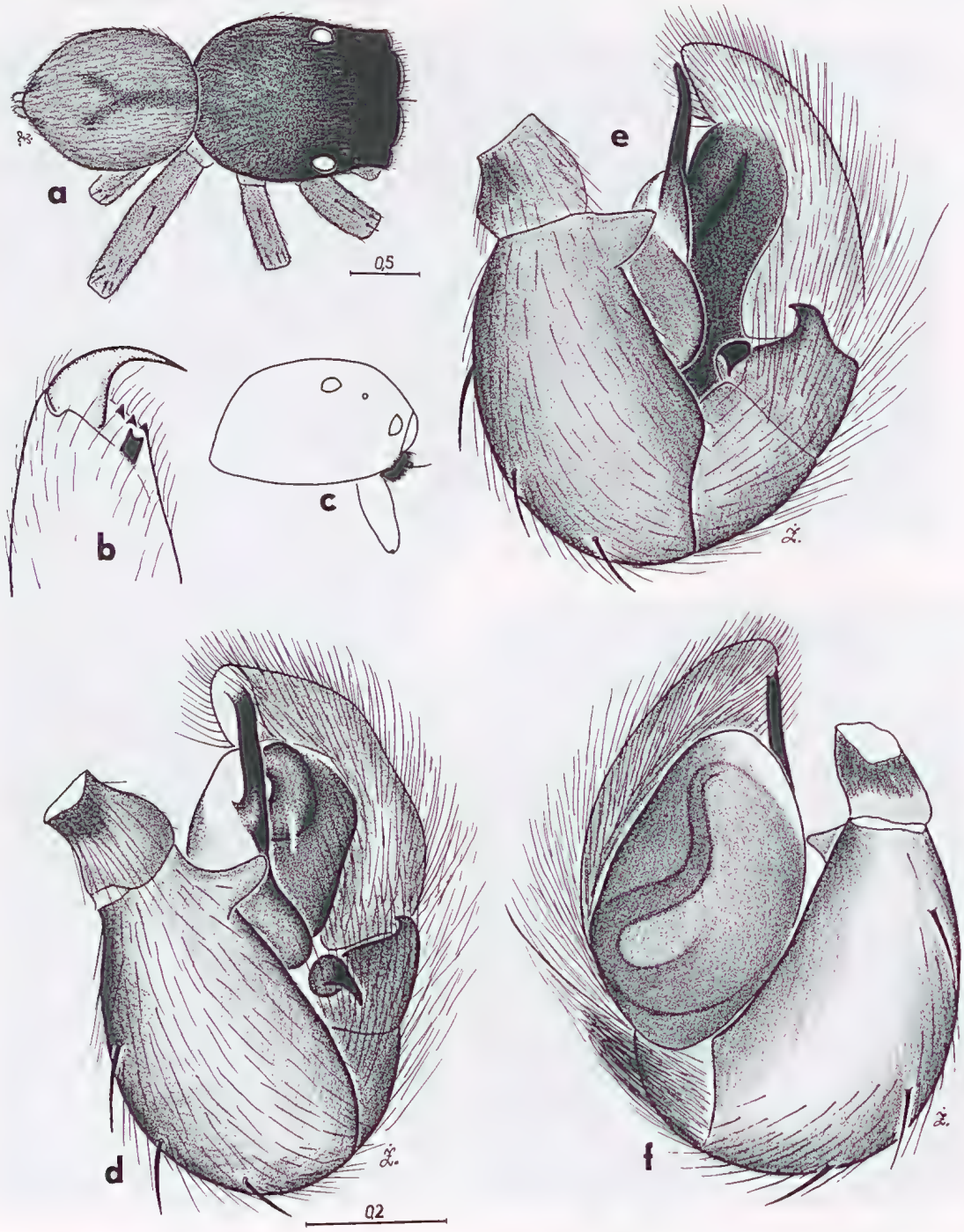


Fig.14. Male *Grayenulla waldockae* n.sp.: general appearance (a), cheliceral dentition (b), lateral view of cephalothorax (c), retrolateral (d-e) and prolateral (f) aspects of palpal organ of the holotype.

comparison to *G. dejongi* tegular spots missing and tibial apophyses of different shape.

Male (Fig.15d). Eye field dirty-brown with black surroundings of eyes. Thorax lighter. Abdomen generally similar to *G. wishartorum*, beige, darker along its anterior median part, with lighter spots posteriorly. Spinnerets beige. Clypeus yellowish, chelicerae (Fig.15e) dirty-yellow. Maxillae and labium honey-yellow with lighter tips. Sternum dirty with whitish hairs, less numerous than in *G. wishartorum*. Legs I hairier than others, their proximal segments yellowish, tibiae and proximal metatarsi dirty-orange, tarsi distally dark. Other legs slightly lighter, joints area darker.

Palpal organ as illustrated in Figure 15b-c.

Dimensions (holotype). CL 1.75, CW 1.40, CH 0.93, EFL 0.85, AEW 1.21, PEW 1.16, AL 1.50.

The female is unknown.

Grayenulla nova n.sp.

Fig.16, Map 2

Material examined. Western Australia, HOLOTYPE, female, Lake Cronin, Mallee/Triodia, LCR, pitfall trap, 6-11 Oct. 1980, W.F. Humphreys *et al.*, WAM 88/2149.

Diagnosis. Species larger than other

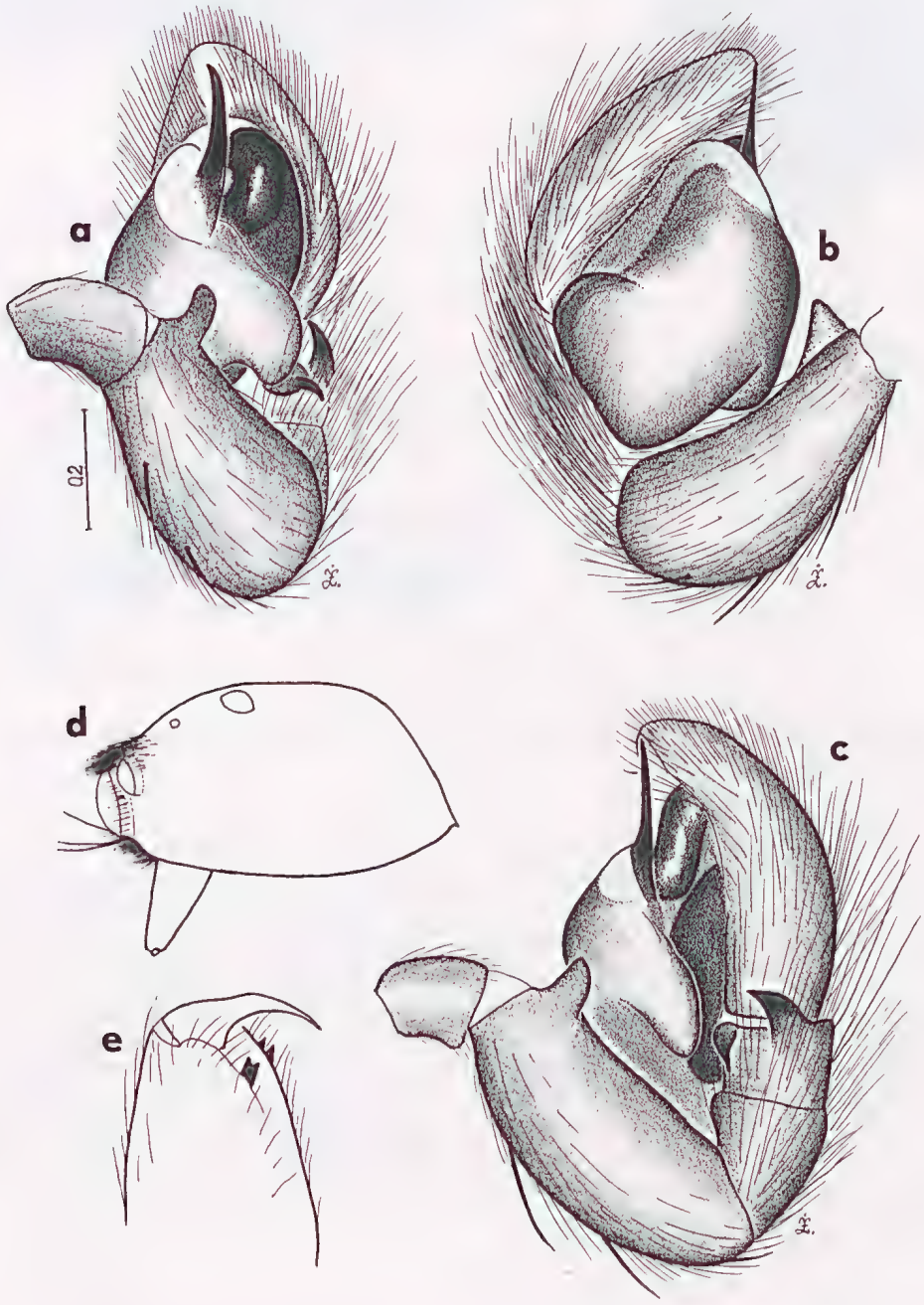


Fig.15. Male *Grayenulla australensis* n.sp.: ventral (a), prolateral (b) and retrolateral (c) aspects of palpal organ, lateral aspect of cephalothorax (d) and cheliceral dentition (d) of the holotype.

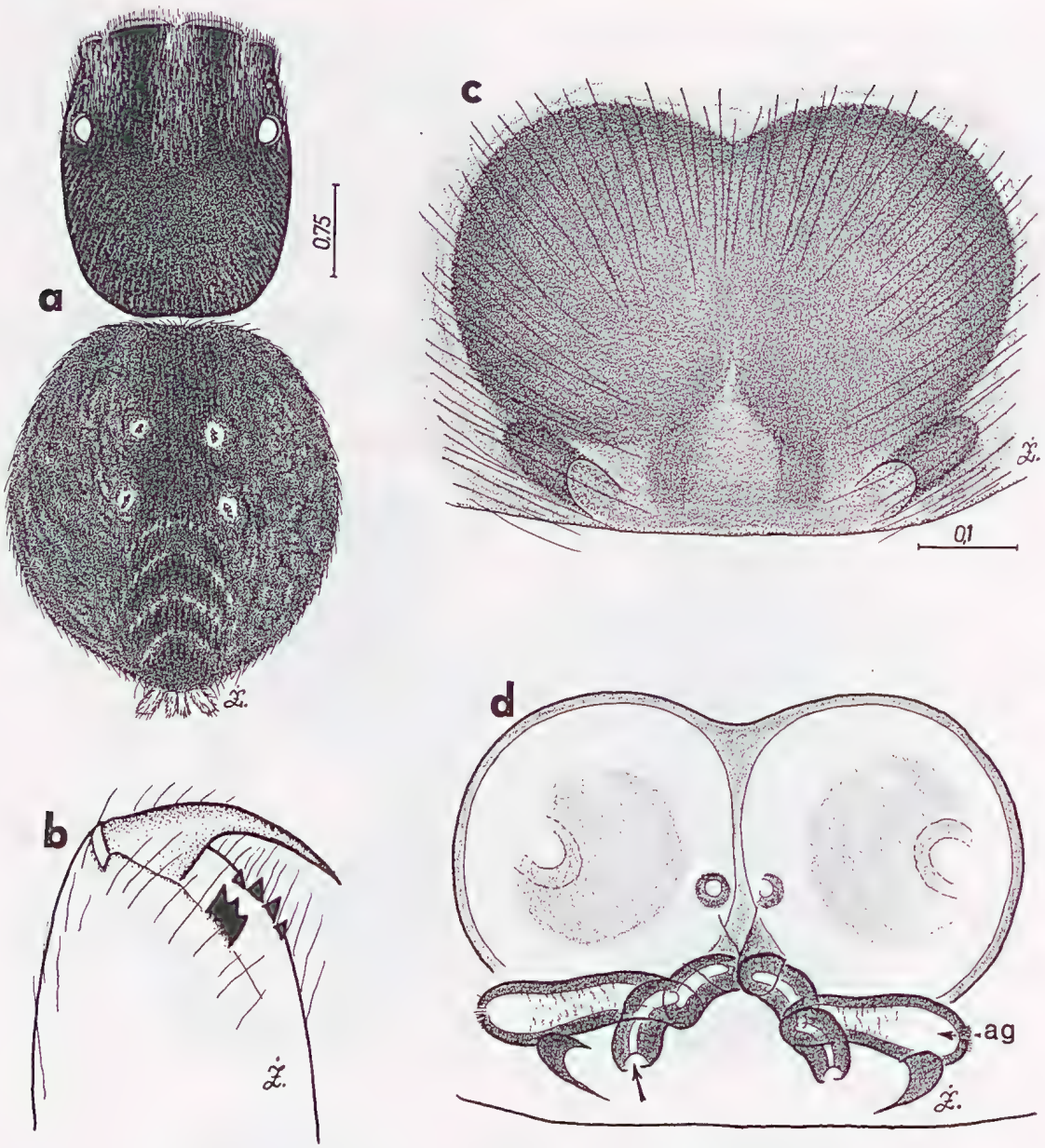


Fig.16. Female *Grayenulla nova* n.sp.: general appearance (a), cheliceral dentition (b), epigyne (c) and internal genitalia (d) of the holotype.

representatives of the genus, accessory glands of epigyne much longer and insemination ducts shorter than in *G. dejongi*.

Female (Fig.16a). Cephalothorax brown, surrounding of eyes darker. White hairs numerous on eye field and lateral surfaces. Abdomen robust, dirty-grey with 4 lighter spots. Clypeus orange with whitish hairs. Chelicerae (Fig.16b) dark-orange. Pedipalps yellow. Maxillae and labium dirty-orange, sternum darker. Venter light with dark-grey spots. Legs orange with grey bands.

Epigyne as illustrated in Figure 16c-d.

Dimensions. CL 1.90, CW 1.70, CH 0.85, EFL 0.75, AEW 1.35, PEW 1.30, AL 2.40.

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A Revision of the Genus *Ichnopus* (Crustacea: Amphipoda: Lysianassoidea: Uristidae)

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Abstract. The uristid genus *Ichnopus* is revised and *Glycerina* included in its synonymy. A key is provided to the world species. *Ichnopus pelagicus* Schellenberg, *I. pseudoserricrus* Ledoyer, *I. serricrus* Walker, *I. spinicornis* Boeck, *I. taurus* Costa, (type species), *I. tenuicornis* (Haswell), *I. teretis* (Andres) and *I. woodmasoni* (Giles) are redescribed. The new species *I. annasona, I. capricornus, I. caritus, I. comorensis, I. cribensis, I. malpatun, I. parriwi* and *I. wardi* are described. *Ichnopus nossibeensis* Ledoyer is considered to be a synonym of *I. pelagicus. Ichnopus macrobetomma* Stebbing is considered to be an unrecognisable species. Two species groups are recognised: the *I. spinicornis* group, in which the ischium and carpus of gnathopod 1 are long and most species are pelagic, probably micropredators; and the *I. taurus* group, in which the ischium and carpus of gnathopod 1 are very long and most species are demersal scavengers. *Ichnopus* is considered to be a tropical to warm temperate Indo-Pacific genus with some remnants in the Mediterranean and the eastern North Atlantic Ocean. The most primitive species in both groups are found in the Mediterranean Sea and the eastern North Atlantic. It appears that the modern genus had its origins in the old Tethyan fauna.

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Ichnopus is a poorly known genus of uristid lysianassoids which was established by Costa (1853) for *I. taurus* from the Mediterranean Sea. Since then 13 species have been described, five of which are currently considered to be synonyms. Most of these species have been reported in the literature only once or twice. The exceptions are *I. taurus* Costa, 1853, and *I. spinicornis* Boeck, 1861, both of which have been recorded frequently, either from the Mediterranean or the eastern North Atlantic. Little is known about the biology, phylogeny or zoogeography of these animals.

In this paper we redefine the genus, recognise two informal species groups, discuss the habitat preferences of species in each group and discuss the general zoogeographical distribution of the genus. We redescribe eight species and describe eight new species. The genus *Glycerina* Haswell, 1882, is synonymised with *Ichnopus* Costa, 1853, and *I. nossibeensis* Ledoyer, 1986, is synonymised with *I. pelagicus* Schellenberg, 1926. *Ichnopus macrobetomma* Stebbing, 1917 is considered to be an unrecognisable species.

The following abbreviations are used in the text:

AM – Australian Museum, Sydney; BMNH – British Museum (Natural History), London; CSIRO – Commonwealth Scientific and Industrial Research Organisation, Division of Fisheries Research, Hobart; MCSN – Museo Civico di Storia Naturale, Verona; MNHN – Museum National d'Histoire Naturelle, Paris; NMV – Museum of Victoria, Melbourne; NMW – Naturhistorisches Museum, Vienna; SAM – South African Museum, Cape Town; SMF – Forschungsinstituts Senckenberg, Frankfurt am Main; USNM – United States National Museum of Natural History, Washington, D.C.; ZMA – Zoölogisch Museum, Amsterdam; ZMB – Zoologisches Museum, Berlin; ZMC – Zoologisk Museum, Copenhagen; ZMUB – Zoologisk Museum, Universitetet i Bergen.

The following abbreviations are used on the plates: A – antenna; EP – epimeron; G – gnathopod; H – head; MD – mandible; MDP – mandibular palp; MP – maxilliped; MPIP – maxilliped inner plate; MPOP – maxilliped outer plate; MPP – maxilliped palp; MX – maxilla; MX1IP – maxilla 1 inner plate; MX1OP – maxilla 1 outer pate; MX1P – maxilla 1 palp; P – peraeopod; T – telson; U – uropod; UL – upper lip; l – left; r – right.

Generic Placement

This study has a phylogenetic basis and cladistic terminology is used throughout, but only the taxonomy of the group is presented here. The phylogenetic and biogeographical analyses will appear in another paper.

Ichnopus belongs to the anonychine group of uristid lysianassoids. The Uristidae, as defined here, comprises taxa with a 7/4 crown spine-tooth arrangement on the outer plate of maxilla 1. Within the Uristidae the anonychine group is characterised by having a mandibular molar which is a setose tongue with no triturating surface. It contains the genera *Anonyx* Krøyer, *Ichnopus* Costa, and *Kyska* Shoemaker.

The 7/4 crown arrangement may be derived from a simple 7/4 arrangement (Fig. 1a) in which 11 distal spine-teeth on the outer plate of maxilla 1 occur in two rows, an apical row of seven spine-teeth (known as ST1 to ST7) and a subapical row of four spine-teeth (known as STA to STD). In the 7/4 crown arrangement (Fig.1b) the outer plate becomes apically narrowed so that some spine-teeth are displaced down the face of the outer plate. The outer row (containing STA and ST1 to ST6) is curved around the distal margin of the plate and the inner row (containing STB to STD and ST7) extends down the medial face of the plate. The movement of ST7 can be traced from a position opposite STD in *Kyska* to a position beyond STD in *Anonyx* and *Ichnopus*.

The monophyly of *Ichnopus* is based on the following synapomorphies: posterodistal tooth on article 1 of the peduncle of antenna 1; setae or spines in the posterodistal area of the callynophore; distinctive shape of mandibular palp article 3; broadening of maxillipedal palp article 2; unusually long ischium of gnathopod 1;

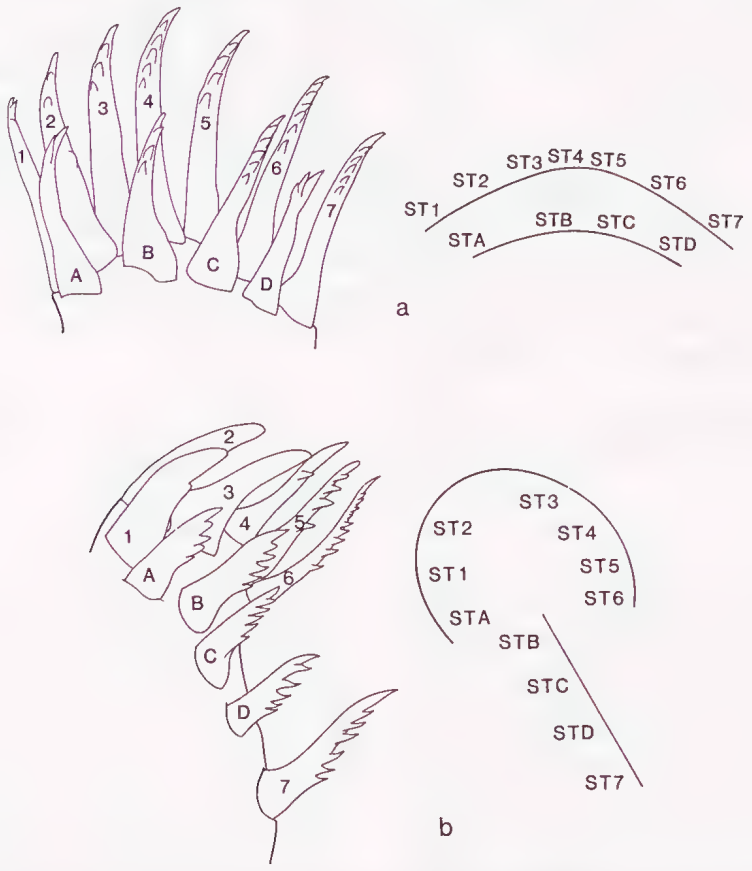

Fig.1. Spine-teeth of maxilla 1 outer plate. a: simple 7/4 arrangement; b: 7/4 crown arrangement.

distinctive cuticular spines on the dactylus of gnathopod 1; and posteroventral notch on epimeron 3.

Ichnopus is divided into two species groups – the *Ichnopus spinicornis* species group and the *Ichnopus taurus* species group. The *I. spinicornis* species group is characterised by: gnathopod 1 with a long ischium and carpus (2.4-2.7 times as long as broad), and short cuticular teeth on the dactylus; a slightly broadened mandibular palp article 2; a medially cuspidate ST7 on the outer plate of maxilla 1; and a strongly spinose molar, except for *I. spinicornis* and *I. comorensis*. Species in the *I. spinicornis* group are: *I. annasona, I. comorensis, I. malpatun, I. pelagicus, I. pseudoserricrus, I. serricrus, I. spinicornis, I. wardi* and *I. woodmasoni*.

The *Ichnopus taurus* species group is characterised by: gnathopod 1 with very long ischium and carpus (4-5.8 times as long as broad), with long cuticular teeth on the dactylus; a strongly broadened mandibular palp article 2; a distally cuspidate ST7 on the outer plate of maxilla 1; and a weakly to moderately spinose molar. Species in the *I. taurus* species group are: *I. caritus, I. capricornus, I. cribensis, I. parriwi, I. taurus, I. tenuicornis, I. teretis* and *Ichnopus* sp. of Walker (1904).

Ecology

Ichnopus spinicornis Species Group

Most species in the *I. spinicornis* species group are entirely or at least partially pelagic and may be micropredators in the plankton. Repelin (1978) reported *I. pelagicus* from the tropical western Pacific Ocean. He found that it was an uncommon amphipod confined to the epipelagic zone (above 150 m) where it was most often collected at night. We report *I. pelagicus* from plankton samples taken at night (between 50 and 100 m) in the Austral Isles, central South Pacific. Working in the south-western Indian Ocean Ledoyer (1986) reported *I. pelagicus* (as *I. nossibeensis*) from plankton samples near the surface in nearly 2000 m of water. He also reported *I. pseudoserricrus* from plankton samples collected near the surface in 29 m of water in the same area. Walker (1909) originally reported two specimens of *I. serricrus*, one from surface plankton and one from a dredge. Echelman & Fishelson (1990a, 1990b) reported *I. serricrus* (males and juveniles) from surface plankton samples taken at night, off reef faces, in the northern Gulf of Aqaba. We report *I. annasona* from surface plankton samples taken at night near Elizabeth Reef in the western Tasman Sea (all males), from epipelagic plankton samples taken at night among the Austral Isles, central South Pacific (males and females), and from epibenthic dredge samples on the Taupo Seamount, western Tasman Sea and near New Caledonia. Kaartvedt (1989) recently reported large numbers of *I. spinicornis* (males and females equally represented) from nocturnal plankton samples in Masfjorden, Norway. However, *I. spinicornis* has also been taken from bottom dredge samples (Chevreux, 1900; Vader, 1969; Marques & Bellan-Santini, 1985; Ledoyer, 1977). Three species with the characters of the *I. spinicornis* group, but with deeply incised basis on peraeopod 5 (a character of the *I. taurus* species group), appear to be demersal. *Ichnopus malpatun* is known from one trap sample taken on the outer reef face at Madang Lagoon, northern Papua New Guinea. An attempt to collect more specimens with a nocturnal plankton tow from a small boat was unsuccessful. *Ichnopus wardi* and *I. woodmasoni* are only known from bottom dredge samples.

Ichnopus taurus Species Group

We consider the species in the *I. taurus* species group to be mainly demersal scavengers. Although their morphology is similar to members of the *I. spinicornis* species group, they are frequently reported from baited traps and as far as we know have never been collected in plankton samples. For instance, we now know that Spandl's (1924) records of *I. taurus* from pelagic samples in the Red Sea represent *I. serricrus*.

Ichnopus taurus has been reported from baited traps in the Mediterranean Sea (Chevreux, 1895, 1903). *Ichnopus teretis* was taken in deep sea traps in the Red Sea (Andres, 1981). In Australian waters *I. capricornus* and *I. parriwi* have only been taken in baited traps. *Ichnopus tenuicornis* has been taken in baited traps on the Great Barrier Reef and in dredge samples on the North West Shelf, Western Australia. Traps have not been set at this location. *Ichnopus caritus* is known only from benthic dredge samples. *Ichnopus cribensis* has been taken in benthic samples and baited traps. *Ichnopus tenuicornis* and *I. capricornus*, which are both common at Lizard Island, Great Barrier Reef, have never been taken in neuston or plankton samples or in pelagic light traps set at night (unpublished data).

To what degree the *I. taurus* group are scavengers we do not know. Sainte-Marie (1986) has shown that, in species where feeding behaviour has been studied in detail, several strategies in addition to carrion feeding usually exist in any one species. Because species such as *I. capricornus* and *I. parriwi* do little damage to the bait even when feeding in large numbers (Keable, personal communication and personal observation) it is possible that they are opportunistic carrion feeders.

Species of the *I. taurus* species group, like its sister taxon *Anonyx*, are mainly demersal scavengers and it is postulated that the common ancestor of these groups was a demersal scavenger. Within the *I. taurus* species group the most significant morphological changes are the long slender gnathopod 1 with its strongly toothed dactylus, the fork-like spine-tooth 7 on maxilla 1 and the deeply serrate posterior margin of the basis on peraeopod 5. It is possible that the modifications to gnathopod 1 are directly related to securing food during scavenging. The same is probably true for spine-tooth 7, but we cannot

easily see a function for the deeply serrate margin of the peraeopod 5 basis.

Apparently at sometime in the early history of *Ichnopus* a demersal scavenger became pelagic. This must have occurred before gnathopod 1 became very slender because all species in the *I. spinicornis* species group have a relatively unmodified gnathopod 1 and spine-tooth 7. The main modification in this group is the strongly spinose mandibular molar. Spination in the molar of the *I. taurus* group is absent or weak. It is also absent in *Anonyx* where the molar is considered to act as a tongue for moving pieces of flesh into the mouth (Dahl, 1979). The modified spinose molar of the *I. spinicornis* group is probably used in the same way as a triturating molar, for tearing or grinding microplanktonic prey.

Zoogeography

Ichnopus is basically a shallow water tropical to warm temperate genus of the Pacific and Indian Oceans (Fig.2). Except for the enigmatic *I. spinicornis*, which occurs in the Mediterranean Sea and in eastern North Atlantic waters as far north as Norway, the *I. spinicornis* species group does not occur outside tropical waters. The more primitive species occur in the eastern North Atlantic Ocean, the Red Sea and the western Indian Ocean and the more advanced species occur in Australian waters. One of the most advanced species, *I. pelagicus*, has an Indo-Pacific distribution.

The *I. taurus* species group is almost entirely confined to the tropical and temperate waters of the western Pacific and Indian Oceans. The one exception, *I. taurus*, occurs in the Mediterranean Sea and in eastern North Atlantic waters as far north as the Bay of Biscay. In southern temperate waters there are three species on the southern coasts of Australia and one species reported from southern Africa. The more primitive species occur in the eastern North Atlantic, Mediterranean Sea and the Red Sea, and the more advanced species occur in the shallow coastal waters of Australia.

Aside from the limited intrusion of *I. spinicornis* and *I. taurus*, the genus has not penetrated the Atlantic Ocean. No species has been found along the well-studied east coast of North America or in the Caribbean Sea. There are no records of *Ichnopus* from the South Atlantic. In the North Pacific there is one record of *I. taurus* from southern Japanese waters (Nagata, 1965). We doubt that this record is *I. taurus* (specimens were not available for study), but it does signal the presence of a species in the *I. taurus* group in the warm western North Pacific. There are no records of *Ichnopus* from the well-studied west coast of North America. *Ichnopus pelagicus* is the only species recorded from the eastern Pacific.

Ichnopus teretis is the only confirmed deep sea species, from 1869 m depth in the central Red Sea. However, Chevreux (1895) reported *I. affinis* (considered to be a synonym of *I. taurus)* from a trap sample at 2620 m depth in the eastern North Atlantic. Unfortunately, these specimens appear to be lost (Mme Defaye, MNHN Paris, *in litt.*). It is possible that *I. affinis* is a valid species, or that the material studied by Chevreux represents an undescribed species.

Ichnopus and *Anonyx* both have species which are scavengers and/or predators. The distribution of the two genera is mutually exclusive except in Norway. *Anonyx* is a northern circumpolar genus with its greatest species diversity in the northern North Pacific (Steele, 1979).

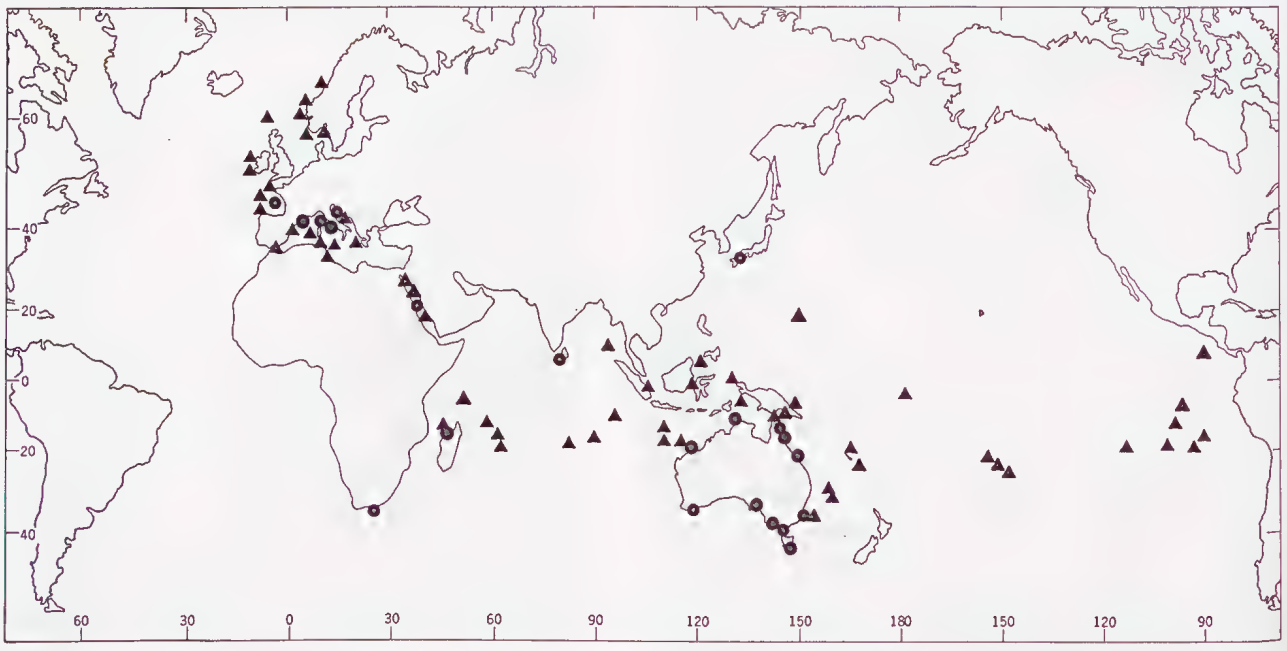

Fig.2. World distribution of the uristid genus *Ichnopus*. Collection areas for the *I. spinicornis* species group are represented by triangles. Collection areas for the *I. taurus* species group are represented by circles.

Systematics

The species diagnoses presented here are based on 17 characters which have been polarised using the outgroup *Anonyx*. *Anonyx* has been thoroughly revised by Steele & Brunel (1968) and is considered to be the sister group of *Ichnopus*. Because the relationships between taxa at any level within the Lysianassoidea are so poorly known we have not formally extended the search for character polarity beyond the immediate sister group. However, the justification for a plesiomorphic state usually goes beyond the outgroup. For instance, outside and within the Uristidae, taxa with fully triturating molars exist and this state is always considered plesiomorphic to a smooth setose tongue molar. A similar case can be made for the constricted inner ramus of uropod 2. It occurs outside and within the Uristidae and is considered plesiomorphic. The character states are shown in Figure 3, and their occurrences are summarised in Table 1.

Character Description and Polarisation

The characters are arranged as they appear in the diagnoses.

1. *Antenna 1, peduncle, anteroventral tooth.* In *Anonyx nugax* there is no anteroventral tooth on peduncular article 1 of antenna 1 (plesiomorphic). In *Ichnopus* most species have a long anteroventral tooth (apomorphic) (Fig.3, 1a). Occasionally it is short (Fig.3, 1b) or absent (Fig.3, 1c).

2. *Antenna 1, callynophore, setae or spines.* In the plesiomorphic state neither setae nor spines occur on the

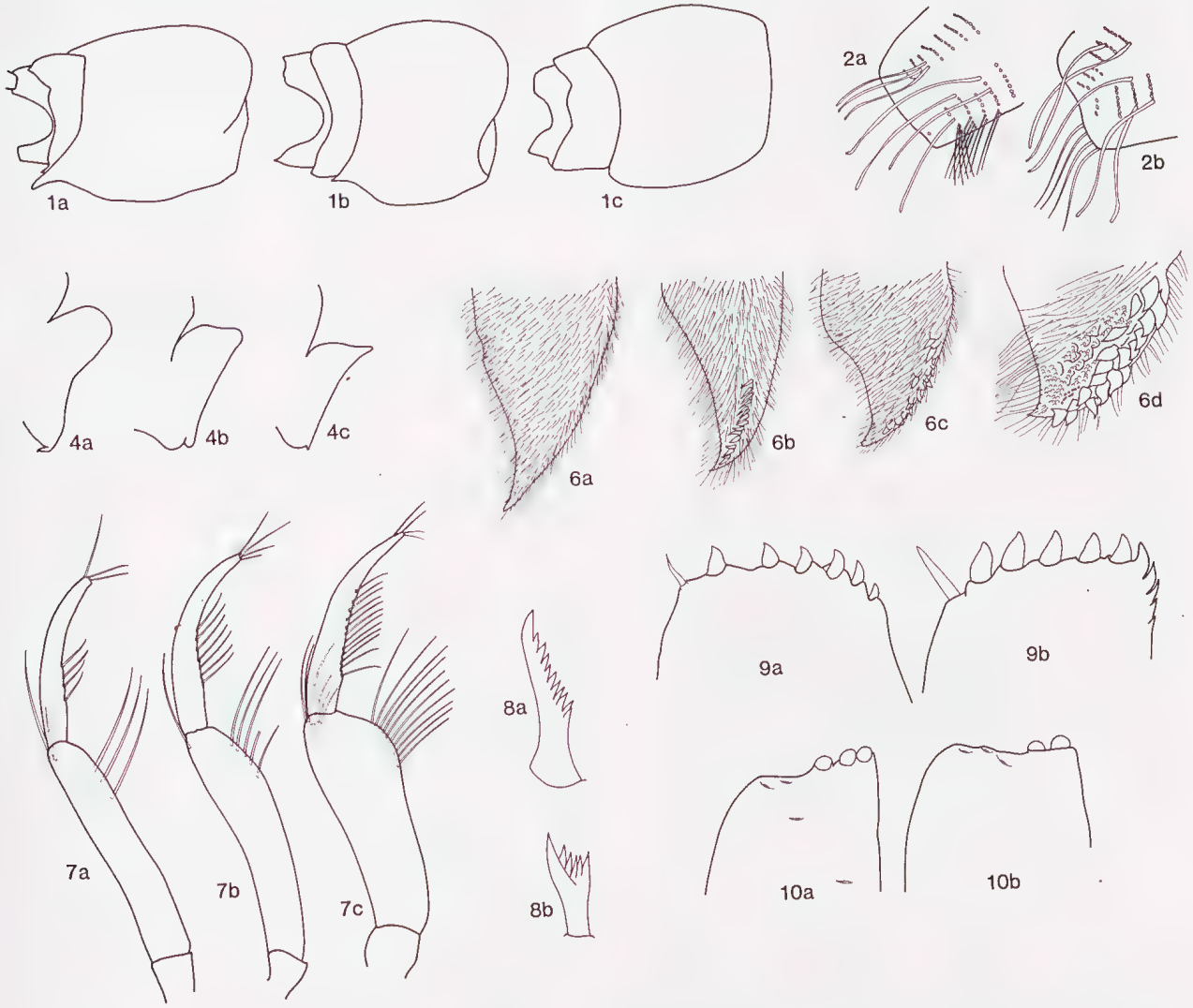

Fig.3a. Taxonomic character states. Antenna 1, peduncular article 1 with long anteroventral tooth (1a); with short anteroventral tooth (1b); without anteroventral tooth (1c). Antenna 1, callynophore with posterodistal setae (2a); with posterodistal spines (2b). Upper lip in profile produced, rounded (4a); produced, subacute (4b); produced, acute (4c). Mandibular molar setose (6a); slightly spinose (6b); moderately spinose (6c); strongly spinose (6d). Mandibular palp article 2 slender (7a); slightly broadened distally (7b); strongly broadened distally (7c). Maxilla 1 with spine-tooth 7 medially cuspidate (8a); distally cuspidate (8b). Maxilla 1 with palp inner distal margin smooth (9a); serrate (9b). Maxilliped, inner plate with 3 nodular spines (10a); with 2 nodular spines (10b).

callynophore. However, according to Steele and Brunel (1968), *Anonyx compactus* Gurjanova, 1962 has a posterodistal spine on the callynophore. In some species of *Ichnopus* setae occur in small rows, similar to the arrangement of aesthetascs, just above the posterior margin (Fig.3, 2a). In other species spines occur on the distal margin just above the posterodistal corner (Fig.3, 2b). These spines are considered to be transformed setae.

3. *Antennae 1 and 2, calceoli.* In *Anonyx* calceoli occur only in mature males (plesiomorphic). In *Ichnopus* calceoli occur either in mature males only or in both males and females (apomorphic). In one species of *Ichnopus* calceoli have not been found in the male, but it is likely that mature males are not known.

4. *Upper lip.* In *Ichnopus* the upper lip/epistome is always separate. In most species of *Ichnopus* the upper lip, in profile, is produced and rounded (plesiomorphic) (Fig.3, 4a). In one species the upper lip is produced but subacute (apomorphic) (Fig.3, 4b); in several other species it is produced and acute (apomorphic) (Fig.3, 4c).

5. *Mandible, lacinia mobilis.* In *Anonyx nugax* the left lacinia mobilis is present as a small slender spine. In *Ichnopus* the left lacinia mobilis may be present as a small slender spine (plesiomorphic), or absent (apomorphic). It has probably been lost at least once in each species group.

6. *Mandible, molar.* The mandibular molar is a setose tongue in *Anonyx* and occasionally in *Ichnopus* (plesiomorphic) (Fig.3, 6a), but usually it is a setose tongue with one of three apomorphic states: weakly spinose (Fig.3, 6b), moderately spinose (Fig.3, 6c) or strongly spinose (Fig.3, 6d). Dahl (1979) and Saint-Marie (1984) have both discussed the highly derived setose tongue of scavenging lysianassoids such as *Anonyx*. Saint-Marie (1984) has discussed the differences between these molars and the triturating molars of less efficient scavengers such as *Orchomenella pinguis* and *Psammonyx nobilis* and illustrated them with SEM. Saint-Marie considered that rasp-like scales on the molar of *O. pinguis* originated from setae. Oshel &

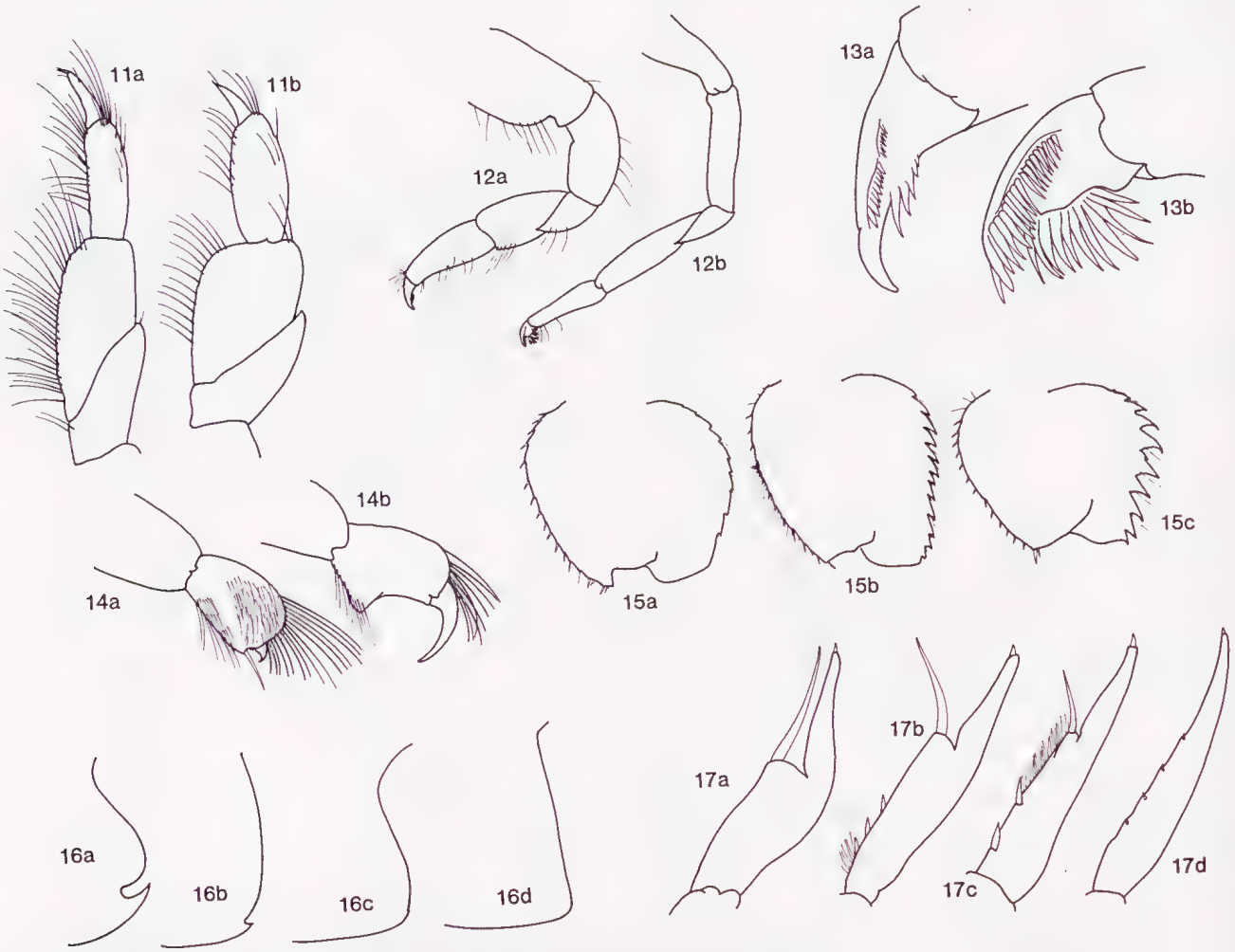

Fig.3b. Taxonomic character states. Maxilliped, palp with broad article 2 (11a); with very broad article 2 (11b). Gnathopod 1 with long ischium and carpus (12a); with very long ischium and carpus (12b). Gnathopod 1 dactylus with short cuticular teeth (13a); with long cuticular teeth (13b). Gnathopod 2 palm and dactylus minute (14a); enlarged (14b). Peraeopod 5 basis with minutely crenate posterior margin (15a); with strongly crenate margin (15b); with deeply serrate margin (15c). Epimeron 3 with large notch (16a); with small notch (16b); with minute notch (16c); with notch absent (16d). Uropod 2 inner ramus strongly constricted (17a); moderately constricted (17b); weakly constricted (17c); not constricted (17d).

Steele (1988) have discussed the comparative morphology of amphipod setae. They consider that 'spines' are merely stout setae and that setae are "...produced by the actions of specialised cells, each of which forms a particular part of the socket-and-seta complex...". In all cases the 'spines' on the *Ichnopus* molar are obviously articulating. In no cases do the 'spines' on the molar bear any resemblance to the triturating molar of other uristids such as *Uristes*. These 'spines' are more similar to setae and are probably derived from the setae of the molar. We therefore consider the spinose state of the setose molar to be a derived condition which reflects a changed function for the molar.

7. *Mandible, palp.* Mandibular palp article 2 may be slender (plesiomorphic) (Fig.3, 7a) to slightly broadened distally (apomorphic) (Fig.3, 7b) or strongly broadened distally (Fig.3, 7c). Occasionally this character is sexually dimorphic, slightly broadened in the female and strongly broadened in the male.

8. *Maxilla 1, spine-tooth 7.* On *Anonyx nugax* spine-tooth 7 is medially cuspidate (plesiomorphic). In *Ichnopus* spine-tooth 7 may have a weak basal cusp with a short medioproximal margin (medially cuspidate, plesiomorphic) (Fig.3, 8a), or a strong basal cusp with a long medioproximal margin (distally cuspidate, apomorphic) (Fig.3, 8b).

9. *Maxilla 1, palp inner margin.* In *Anonyx nugax*, and several species of *Ichnopus*, the inner margin of the maxilla 1 palp is smooth (plesiomorphic) (Fig.3, 9a). In most species of *Ichnopus* it is serrate (apomorphic) (Fig.3, 9b).

10. *Maxilliped, inner plate nodular spines.* In *Anonyx nugax* and most lysianassoids there are 3 small nodular spines on the distal margin of the inner plate (plesiomorphic) (Fig.3, 10a). In some species of *Ichnopus* there are only 2 nodular spines (apomorphic) (Fig.3, 10b).

11. *Maxilliped, palp.* The second article of the maxillipedal palp is slender in *Anonyx* (plesiomorphic), but it is broad (Fig.3, 11a) or very broad (Fig.3, 11b) in all species of *Ichnopus*.

12. *Gnathopod 1, ischium and carpus.* In *Anonyx*, which has a subchelate gnathopod 1, the ischium of gnathopod 1 is short and the carpus is long (plesiomorphic). In *Ichnopus*, which has a simple gnathopod 1, the ischium and carpus may be long (carpus 2.4 to 2.7 times as long as broad) (Fig.3, 12a) or very long (carpus 4.0 to 5.8 times as long as broad) (Fig.3, 12b).

13. *Gnathopod 1, dactylus.* In *Anonyx* the dactylus of gnathopod 1 never has cuticular teeth (plesiomorphic). In *Ichnopus* the dactylus always bears cuticular teeth. They may be short (Fig.3, 13a) or long (Fig.3, 13b).

14. *Gnathopod 2.* In most species of *Ichnopus* gnathopod 2 is minutely subchelate (plesiomorphic), (Fig.3, 14a) but in some species the palm and dactylus become enlarged in the female (apomorphic) (Fig.3, 14b).

15. *Peraeopod 5, basis.* In *Anonyx* and some species of *Ichnopus* the posterior margin of the basis of peraeopod 5 is minutely crenate (plesiomorphic) (Fig.3, 15a). In other species the posterior margin is either strongly crenate (Fig.3, 15b) or deeply serrate (Fig.3, 15c).

16. *Epimeron 3.* Species of *Anonyx* have an acute tooth above the rounded posteroventral corner of epimeron 3, but no notch (plesiomorphic). In *I. spinicornis* there is a large notch (Fig.3, 16a) in this position. In most other species of *Ichnopus* there is a small (Fig.3, 16b) or minute (Fig.3, 16c) notch near the corner, and in *I. teretis* this notch is absent (Fig.3, 16d).

17. *Uropod 2, inner ramus.* This character has four states: strongly constricted (Fig.3, 17a), moderately constricted (Fig.3, 17b), weakly constricted (Fig.3, 17c) and non-constricted (Fig.3, 17d). Steele (1979) considered that the plesiomorphic condition was non-constricted, which he argued was found in many other lysianassoids. From this condition he derived four variously constricted states. In *Anonyx* and in more distantly related taxa such as *Hirondellea*, the lysianassids and the amaryllidids, constricted and non-constricted states occur. It is more parsimonious to consider the constricted inner ramus of uropod 2 as plesiomorphic and that it is variously reduced or lost in different lineages; otherwise the constricted form must re-evolve in several different lineages. Consequently, within *Anonyx* and *Ichnopus* the strongly constricted state is plesiomorphic and its reduction or loss are derived states.

Ichnopus Costa

Ichnopus Costa, 1853: 169.–Costa, 1857: 188.–Boeck, 1871: 98.–Sars, 1890: 39.–Della Valle, 1893: 800 (in part).–Stebbing, 1906: 52.–Chevreux & Fage, 1925: 46.–Stephensen, 1929a: 60.–Pirlot, 1936: 269.–Gurjanova, 1951: 219.–J.L. Barnard, 1969: 346.–Lincoln, 1979: 94.–Ledoyer, 1986: 760.–Diviacco & Ruffo, 1989: 486.–Barnard & Karaman, 1991: 491. [Type species: *Ichnopus taurus* Costa, 1853, by monotypy.]

Glycera Haswell, 1879a: 256 (not *Glycera* Lamarck, 1818, Polychaeta). [Type species: *Glycera tenuicornis* Haswell, 1879, by monotypy.]

Glycerina Haswell, 1882: 233 [*nom. nov.* for *Glycera* Haswell, 1879].–Stebbing, 1906: 60.–Pirlot, 1936: 270.–J.L. Barnard, 1969: 345.–Barnard & Karaman, 1991: 488.

Diagnosis. Antenna 1, peduncular article 1 with posterodistal tooth; callynophore with posterodistal setae or spines. Upper lip/epistome separate, upper lip strongly produced. Mandibular palp with slender, falcate third article. Maxilliped outer plate distomedially truncated. Gnathopod 1 simple, ischium and carpus long or very long, dactylus with cuticular teeth on posterior margin. Peraeopods 3 and 4: males with plumose setae on posterior margin of merus and carpus. Gnathopod 2 to peraeopod 6 with strongly pleated gills, peraeopod 7 with tiny smooth gill.

Description. *Head*: slightly deeper than long, lateral cephalic lobe well developed, narrowly to broadly rounded; rostrum absent; eyes reniform, very slightly enlarged to enlarged and meeting dorsally in reproductive male. *Antenna 1:* medium length, about 0.3 times as long as body, subequal to or up to 0.5 times as long as antenna 2; peduncular article 1 short, from as long as deep to 1.8 times as long as deep, with long posterodistal tooth; accessory flagellum 6- to 10-articulate, not forming cap; callynophore, well-developed 2-field in female and male, with posterodistal setae or spines; flagellum long, 10- to 90-articulate; calceoli present in female and male or in male only. *Antenna 2:* about 0.4 times as long as body, occasionally as long as body in male; peduncle with brush setae in female and male, peduncular articles 4 and 5 not swollen in female or male; calceoli present in female and male or in male only.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded, subacute or acute. *Mandible:* incisors symmetrical with slightly convex margins; left lacinia mobilis a small slender spine or absent; accessory spine row, left with 3 or 4 spines, right with 4 spines, rarely more variable; molar a setose tongue with spines absent to well developed, without triturating surface; mandibular palp attached midway; article 1 short, about as long as broad or twice as long as broad; article 2 elongate, slender to strongly broadened distally, with setae along distal third of medial margin and on distolateral corner; article 3 slender, falcate, without A- or B-setae, with D-setae weakly to strongly developed but always proximal, with E-setae. *Maxilla 1:* inner plate small, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, without cusps or weakly cuspidate, ST4 to ST6 large, slender, multicuspidate, ST7 short or long, displaced from ST6, multicuspidate medially or distally, STA 0- to 4-cuspidate, STB-STC 2- to 5-cuspidate, STD 1- to 6-cuspidate; palp large, 2-articulate, with 4-9 terminal spines and 1 or 2 flag setae. *Maxilla 2:* inner plate about three quarters as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 2 or 3 well-developed nodular spines, oblique setal row reduced, with 3-9 plumose setae; outer plate small to medium in size, subovate, distomedially truncated, apical setae and spines absent, medial spines reduced in size, bead-shaped, submarginal setae vestigial; palp well developed, with article 2 weakly to strongly broadened, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium long to very long (2.0-4.5 times as long as broad); carpus long (2.4-2.7 times as long as broad) or very long (4.0-5.8 times as long as broad); carpus about 1.4 times as long as propodus; propodus long, subrectangular, about 4 times as long as broad, margins subparallel or slightly tapering, posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of medial spines and a row of cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate, occasionally greatly expanded in female; coxa large, subequal in size to coxa 3; carpus long, posterior margin broadly lobate; propodus subrectangular; palm slightly acute, occasionally broadly transverse and concave; posterodistal corner without spines or occasionally with a minute spine.

Peraeopods 3 to *7*: with short, slender dactyli. *Peraeopod 4*: coxa with well-developed posteroventral lobe; male, and sometimes female, merus/carpus with plumose setae. *Peraeopod 5:* coxa bilobate; basis expanded with posterior margin minutely crenate to deeply serrate. *Peraeopod 7:* basis, posterior margin slightly rounded with rounded posteroventral corner and rounded to straight posteroventral margin; merus slender, not expanded posteriorly.

Oostegites: from gnathopod 2 to peraeopod 5. *Gills*: from gnathopod 2 to peraeopod 7, strongly pleated with an expanded sac-like distal end, gill on peraeopod 7 tiny, not pleated.

Epimeron 3: usually with a notched posteroventral corner, notch occasionally absent. *Urosomite 3*: with small dorsolateral spines. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: with few long fine setae; rami subequal in length, inner ramus with or without constriction. *Uropod 3:* peduncle short, 1.3-1.8 times as long as broad, without lateral flange; rami lanceolate, subequal in length, with long fine setae and minutely serrate margins; plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft, without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. We find no reason to retain the generic concept of *Glycerina* Haswell. All species in the genus are characterised by the synapomorphies stated in the diagnosis. Within *Ichnopus* there is a tendency among some advanced species to develop very long slender first gnathopods, deeply serrate basis on peraeopod 5 and in the most advanced species, sexually dimorphic second gnathopods.

Ichnopus is placed in the anonychine group because the spine-teeth of maxilla 1 form a 7/4 crown and the molar is a setose tongue. The synapomorphies which distinguish *Ichnopus* from other anonychine genera are the toothed dactylus of the first gnathopod, the distinctive third article of the mandibular palp and the posterodistal spine on the first peduncular article of antenna 1. Synapomorphies within the genus include spines on the mandibular molar, mandibular palp article 2 broadened distally, distally cuspidate ST7 on maxilla 1, very long ischium and carpus of gnathopod 1, dimorphic second gnathopods, deeply serrate posterior margin on basis of peraeopod 5, and non-constricted inner ramus of uropod 2.

Characters such as the simple gnathopod 1, the strongly pleated gills, the produced, rounded upper lip, medially cuspidate ST7 on maxilla 1, plumose setae on peraeopods 3 and 4 and fine setae on the uropods may indicate a relationship with some socarnine lysianassids.

In this case the 7/4 crown of maxilla 1 would have to be considered as a convergent character. Our analyses to date indicate a stronger affinity with the uristids.

Gnathopod 1 has a superficial similarity to the scopelocheirid gnathopod. However, in *Ichnopus* the dactylus is large and bears rows of cuticular teeth and spines; in scopelocheirids the dactylus is usually tiny and the rows of setae and cuticular spines arise mostly from the propodus. *Schisturella* has a posterodistal spine on the callynophore, but this is considered as a homoplastic character. Posterodistal setae also occur on the callynophore of *Podoprion*, which also has a deeply serrate basis on peraeopod 5, but many other characters indicate that the two genera are not closely related and the characters are considered homoplastic.

Within the anonychine group *Anonyx* differs from *Ichnopus* in not having a strong posterodistal tooth on the peduncle of antenna 1, posterodistal setae or spines on the callynophore or a strongly produced upper lip, and in having article 3 of the mandibular palp long, broad and falcate with D-setae along most of its margin, a subchelate gnathopod 1 with a short ischium, no posterior setae on the merus and carpus of peraeopods 3 and 4, and plumose setae on the rami of uropod 3 in females and males. *Kyska* Shoemaker differs from *Ichnopus* in not having a strong posterodistal tooth on the peduncle of antenna 1 or posterodistal setae or spines on the callynophore, in having a reduced setose molar on the mandible and a chelate gnathopod 1 with short ischium and carpus.

The genus currently contains 16 species: *Ichnopus annasona* n.sp., *I. capricornus* n.sp., *I. caritus* n.sp., *I. comorensis* n.sp., *I. cribensis* n.sp., *I. malpatun* n.sp., *I. parriwi* n.sp., *I. pelagicus* Schellenberg, *I. pseudoserricrus* Ledoyer, *I. serricrus* Walker, *I. spinicornis* Boeck, *I. taurus* Costa, *I. tenuicornis* (Haswell), *I. teretis* (Andres), *I. wardi* n.sp. and *Ichnopus woodmasoni* (Giles). Insufficient information is available to determine the status of *Ichnopus macrobetomma* Stebbing.

Key to Species of *Ichnopus*

1. Gnathopod 1, ischium and carpus long (Fig.3, 12a) 2

—— Gnathopod 1, ischium and carpus very long (Fig.3, 12b) 10

2. Peraeopod 5, posterior margin of basis deeply serrate (Fig.3, 15c) 3

—— Peraeopod 5, posterior margin of basis minutely to strongly crenate (Fig.3, 15a,b) 5

3. Upper lip rounded (Fig.3, 4a) ..... *I. malpatun*

—— Upper lip acutely produced (Fig.3, 4c) 4

4. Gnathopod 2 female, minutely subchelate (Fig.3, 14a) ..... *I. wardi*

—— Gnathopod 2 female, grossly subchelate (Fig.3, 14b) ..... *I. woodmasoni*

5. Uropod 2, inner ramus constricted (Fig.3, 17a-c) 6

—— Uropod 2, inner ramus not constricted (Fig.3, 17d) ..... *I. pelagicus*

6. Peraeopod 5, basis with minutely crenate posterior margin (Fig.3, 15a) 7

—— Peraeopod 5, basis with strongly crenate posterior margin (Fig.3, 15b) 9

7. Epimeron 3 with small or minute posteroventral notch (Fig.3, 16b,c) 8

—— Epimeron 3 with large posteroventral notch (Fig.3, 16a) ..... *I. spinicornis*

8. Mandible, molar strongly spinose (Fig.3, 6d), palp strongly setose; maxilla 1, palp inner margin distally serrate (Fig.3, 9b) ..... *I. annasona*

—— Mandible, molar not spinose (Fig.3, 6a), palp weakly setose; maxilla 1, palp inner margin smooth (Fig.3, 9a) ..... *I. comorensis*

9. Maxilla 1 outer plate, ST7 medially cuspidate (Fig.3, 8a); left mandible with 4 accessory spines ..... *I. pseudoserricrus*

—— Maxilla 1 outer plate, ST7 distally cuspidate (Fig.3, 8b); left mandible with 3 accessory spines ..... *I. serricrus*

10. Antenna 1, callynophore with posterodistal setae (Fig.3, 2a) 11

—— Antenna 1, callynophore with posterodistal spines (Fig.3, 2b) 14

11. Peraeopod 5, basis with deeply serrate posterior margin (Fig.3, 15c) 13

—— Peraeopod 5, basis with minutely crenate posterior margin (Fig.3, 15a) 12

12. Antenna 1, peduncular article 1 with small posterodistal tooth (Fig.3, 1b); mandible, molar with row of small spines, palp article 3 with about 11 proximal D-setae ..... *I. taurus*

—— Antenna 1, peduncular article 1 with rounded posterodistal corner (Fig.3, 1c); mandible, molar with row of large spines, palp article 3 with about 4 proximal D-setae ..... *Ichnopus* sp.

13. Peraeopod 7, basis with straight posteroventral margin (Fig.8); epimeron 3 with small notch on posteroventral corner (Fig.3, 16b) ..... *I. capricornus*

—— Peraeopod 7, basis with rounded posteroventral margin; epimeron 3 without notch on posteroventral corner (Fig.3, 16d) ..... *I. teretis*

14. Antennae with calceoli only in male 15

—— Antennae with calceoli in male and female ..... *I. parriwi*

15. Gnathopod 2, minutely subchelate in male and female (Fig.3, 14a) 16

—— Gnathopod 2, grossly subchelate in female (Fig.3, 14b) ..... *I. tenuicornis*

16. Mandible, molar setose only (Fig.3, 5a) ..... *I. caritus*

—— Mandible, molar setose and weakly spinose (Fig.3, 5b) ..... *I. cribensis*

A summary of the character states for each species is given in Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
***I. spincornis* species group**																	
I. spinicornis	long	+–	++	round	+	absent	strong	medial	smooth	2	broad	long	short	–	+	vlarge	strong
I. pseudoserri	long	+–	+?	round	+	strong	strong	medial	serrate	3	broad	long	short	?	++	small	mod
I. serricrus	long	+–	+–	subac	+	strong	strong	distal	serrate	3	broad	long	short	–	++	small	mod
I. annasona	short	+–	++	round	–	strong	strong	medial	serrate	3	vbroad	long	short	–	+	minute	strong
I. wardi	long	+–	++	acute	–	strong	strong	medial	serrate	2	vbroad	long	short	–	+++	small	strong
I. woodmasoni	long	+–	++	acute	–	strong	strong	medial	serrate	2	vbroad	long	short	+	+++	small	strong
I. comorensis	short	+–	+?	?	+	absent	slender	medial	smooth	2	broad	long	short	?	+	small	strong
I. malpatun	long	+–	++	round	–	strong	strong	medial	serrate	2	broad	long	short	–	+++	small	mod
I. pelagicus	short	+–	++	round	–	strong	strong	medial	serrate	2	vbroad	long	short	–	+	minute	absent
***I. taurus* species group**																	
I. taurus	short	+–	+–	round	+	weak	slight	distal	serrate	3	broad	vlong	long	–	+	small	mod
I. capricornus	long	+–	+–	round	–	weak	slender	distal	serrate	3	broad	vlong	long	–	+++	small	weak
I. teretis	short	+–	––	round	–	absent	slender	distal	serrate	3	broad	vlong	long	–	+++	absent	weak
I. caritus	long	–+	+–	round	–	absent	slender	distal	serrate	3	vbroad	vlong	long	–	+++	small	mod
I. parriwi	long	–+	++	round	–	mod	slight	distal	serrate	3	vbroad	vlong	long	–	+++	small	mod
I. tenuicornis	long	–+	+–	round	–	weak	slight	distal	smooth	3	vbroad	vlong	long	+	+++	small	mod
I. cribensis	long	–+	+–	round	–	weak	slender	distal	serrate	3	vbroad	vlong	long	–	+++	small	mod

Table 1. Distribution of character states in *Ichnopus* species. Character numbers are: 1. Antenna 1, peduncular article 1: tooth; 2. Antenna 1, callynophore: setae or spines; 3. Calceoli: present in males and/or females; 4. Upper lip; 5. Lacinia mobilis: + = present, – = absent; 6. Molar spines; 7. Mandibular palp, article 2: expansion; 8. Maxilla 1, outer plate, spine-tooth 7: cuspidation; 9. Maxilla 1, palp, inner margin; 10. Maxilliped, inner plate: nodular spines; 11. Maxilliped, palp article 2: expansion; 12. Gnathopod 1, ischium and carpus; 13. Gnathopod 1, dactylar teeth; 14. Female gnathopod 2, palm: – = minutely subchelate, + = enlarged, ? = not known; 15. Peraeopod 5, basis, posterior margin: + = minutely crenate, ++ = strongly crenate, +++ = deeply serrate; 16. Epimeron 3, notch; 17. Uropod 2, inner ramus, constriction.

Ichnopus annasona n.sp.

Figs 4-5

Type material. HOLOTYPE, male, 14 mm, AM P39649, 5 male PARATYPES, AM P39650, Elizabeth Reef, Tasman Sea, 29°55'S 159°05'E, hand net at surface, attracted to light at night, A. Gill & J.K. Lowry on RV *Flamingo Bay*, 12 Dec. 1987, site 42; 3 male PARATYPES, AM P39651, Elizabeth Reef, Tasman Sea, 29°58'S 159°03'E, hand net and spot light at night, A. Gill on RV *Flamingo Bay*, Dec. 1987, site 35b.

Additional material examined. Female, AM P40093, off Lord Howe Island, Tasman Sea, 31°38.03'S 159°03.1'E, calcareous nodules, coral sand, some algae, 44 m, dredged, W. Ponder, J.K. Lowry & F.W. Rowe on HMAS *Kimbla*, 6 Nov. 1976, stn LH2; female, 10 mm, MNHN Am 4438, off New Caledonia, 22°53'S 167°17'E, 570-610 m, N.O. *Jean Charcot*, 30 Aug. 1985, BIOCAL stn DW 46; 4 specimens, AM P41008, Taupo Seamount, western Tasman Sea, 33°14.21'S 156°10.68'E, rough marl bottom, 133 m, epibenthic sled, J.K. Lowry *et al.* on RV *Franklin*, 2 May 1989, stn FR 05/89-7; 5 males, 2 females, 1 juvenile, AM P41004, (1 ovigerous female, body translucent, except gut coloured by food, eyes red), off Rurutu, Austral Isles, 22°29'S 151°21'W, plankton tow, 0-50 m, J.M. Poupin & J.K. Lowry on RV *Marara*, 11 Aug. 1991, FRP-20; male, AM P41013, off Tubuai, Austral Isles, 23°19.5'S 149°31.0'W, plankton sample, estimated depth 50 - 100 m, J.M. Poupin & J.K. Lowry on RV *Marara*, 13 Aug. 1991, FRP-37.

Diagnosis. Antenna 1: peduncular article 1 with short posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli present in male and female. Upper lip rounded. Mandible: left lacinia mobilis absent; accessory spine row, left and right each with 4

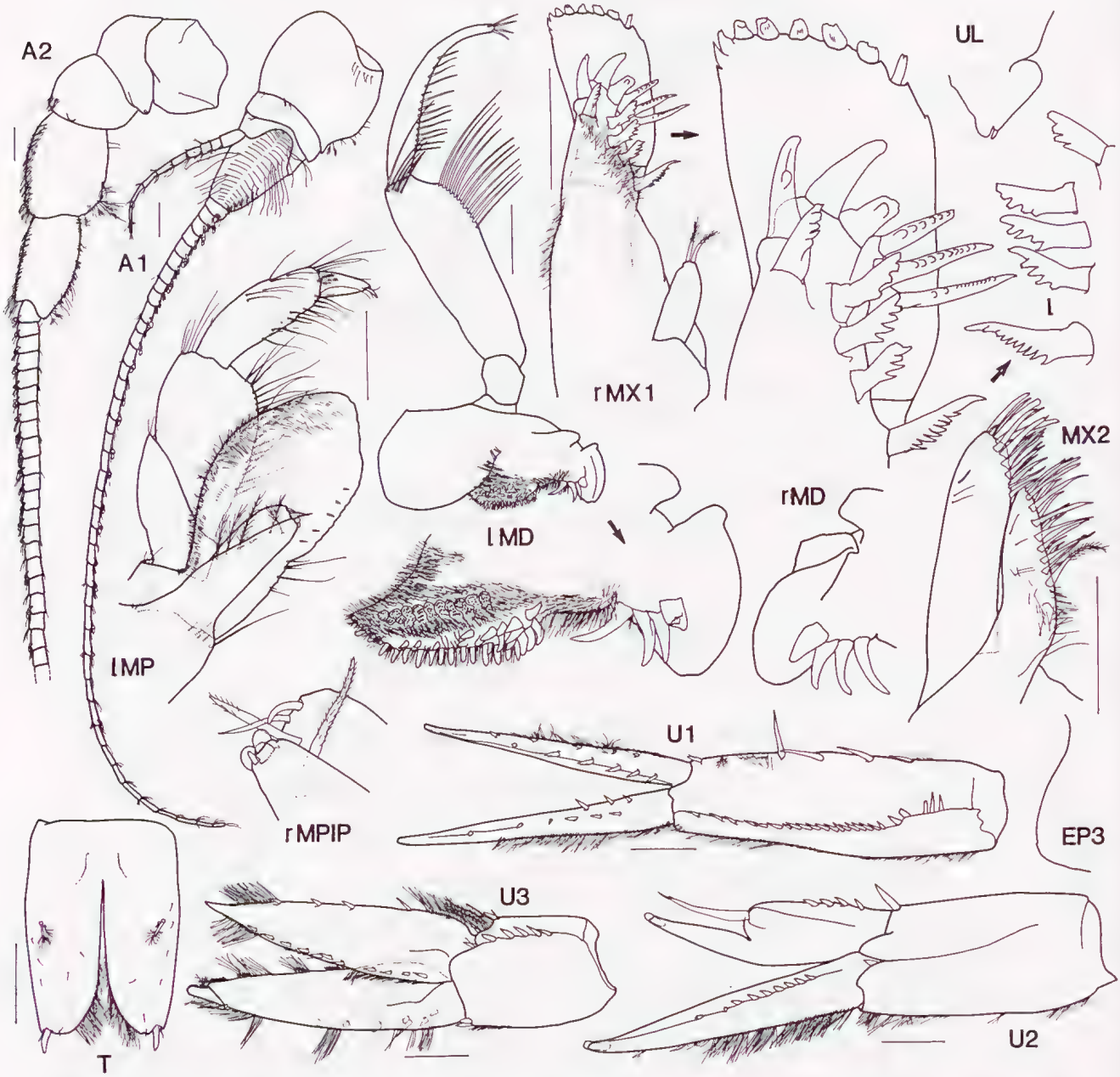

Fig.4. *Ichnopus annasona* n.sp., holotype male, 14 mm, AM P39649, Elizabeth Reef, western Tasman Sea. Scales represent 0.2 mm.

spines; molar setose, strongly spinose; palp article 2 strongly broadened distally. Maxilla 1 with ST7 multicuspidate medially; palp inner margin distally serrate. Maxilliped: inner plate with 3 nodular spines; palp article 2 very broad. Gnathopod 1: ischium and carpus long; dactylus with short cuticular teeth. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin minutely crenate. Epimeron 3: posteroventral corner with minute notch. Uropod 2: inner ramus with strong constriction.

Description. Based on holotype male, 14 mm and female, 10 mm, MNHN Am 4438. *Head* slightly deeper than long, lateral cephalic lobe well developed, broadly rounded; rostrum absent; eyes reniform, enlarged in reproductive male. *Antenna 1*: medium length, about 0.4 times as long as body, about 0.5 times as long as antenna 2; peduncular article 1 short, about as long as broad, with short posterodistal tooth; accessory flagellum 10-articulate, article 1 slightly elongate, 0.1 times as long as flagellum; callynophore well-developed 2-field in female and male, with posterodistal setae; flagellum long, 41-articulate; calceoli present in female and male. *Antenna 2*: up to 0.9 times as long as body in male, 0.4 times in female; peduncle with brush setae in female and male, peduncular articles 4 and 5 not swollen in female or male; calceoli present in female and male.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded. *Mandible*: incisors symmetrical with slightly convex margins; left lacinia mobilis absent; accessory spine row, left and right each with 4 spines; molar setose, strongly spinose; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, strongly broadened distally, with 12 setae along distal third of medial margin and row of 7 setae on distolateral corner; article 3 strongly falcate with 13 proximal D-setae and 4 short E-setae. *Maxilla 1*: inner plate small, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3

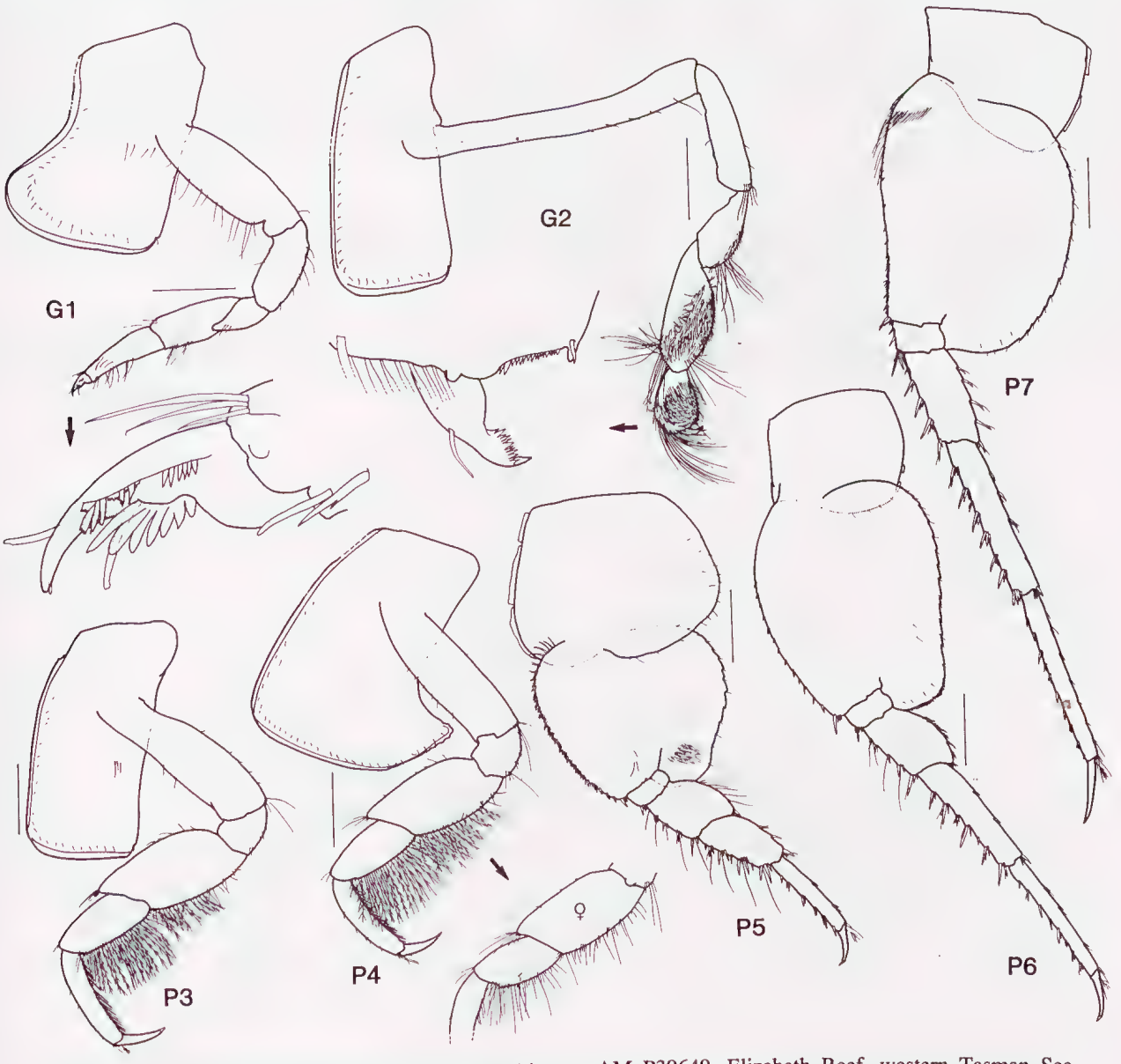

Fig.5. *Ichnopus annasona* n.sp., holotype male, 14 mm, AM P39649, Elizabeth Reef, western Tasman Sea. Scales represent 0.5 mm.

large, stout, weakly cuspidate, ST4 to ST6 large, slender, multicuspidate, ST7 long, multicuspidate medially, STA to STD 3- to 4-cuspidate; palp large, 2-articulate, with 5 terminal spines and 1 flag seta. *Maxilla 2*: inner plate about three quarters as long as outer plate. *Maxilliped*: inner plate large, subrectangular, with 3 well-developed nodular spines, oblique setal row reduced, with 6 plumose setae; outer plate medium size, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, 5 vestigial submarginal setae present; palp well developed, article 2 very broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium long, twice as long as broad; carpus long, 2.3 times as long as broad, 1.1 times as long as propodus; propodus long, 2.8 times as long as broad, tapering distally; posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of about 18 medial spines and a row of 7 cuticular teeth along posterior margin. *Gnathopod 2*: minutely subchelate; coxa large, subequal in size to coxa 3; carpus long, 2.4 times as long as broad, posterior margin broadly lobate; propodus subrectangular, short, 1.6 times as long as broad; palm slightly acute, with straight, minutely serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe; male merus/carpus with plumose setae. *Peraeopod 5*: coxa equilobate; basis expanded with posterior margin minutely crenate. *Peraeopod 7*: basis, posterior margin slightly rounded with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with a minutely notched posteroventral corner. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: with long fine setae; rami subequal in length, inner ramus with strong constriction. *Uropod 3*: peduncle short, 1.6 times as long as broad, without lateral flange; rami lanceolate, subequal in length, with long fine setae and minutely serrate margins, plumose setae absent; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (74%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. *Ichnopus annasona* is in the *I. spinicornis* species group and is considered to be the sister taxon of *I. pelagicus*. It differs from *I. pelagicus* in having 3 nodules on the inner plate of the maxilliped and a strongly constricted inner ramus on uropod 2.

Etymology. Named after the steel barque *Annasona*, wrecked on Middleton Reef in 1907.

Distribution. *Ichnopus annasona* is known from surface pelagic waters to 133 m near Taupo Seamount, Lord Howe Island and Elizabeth Reef in the western Tasman Sea, from surface to 610 m depth off New Caledonia, and surface to 100 m depth in pelagic waters among the Austral Isles in the central south Pacific.

Ichnopus capricornus n.sp.

Figs 6-8

Type material. HOLOTYPE, female, 10 mm, non-ovigerous, AM P39644, 35 PARATYPES, AM P39645, Heron Island,

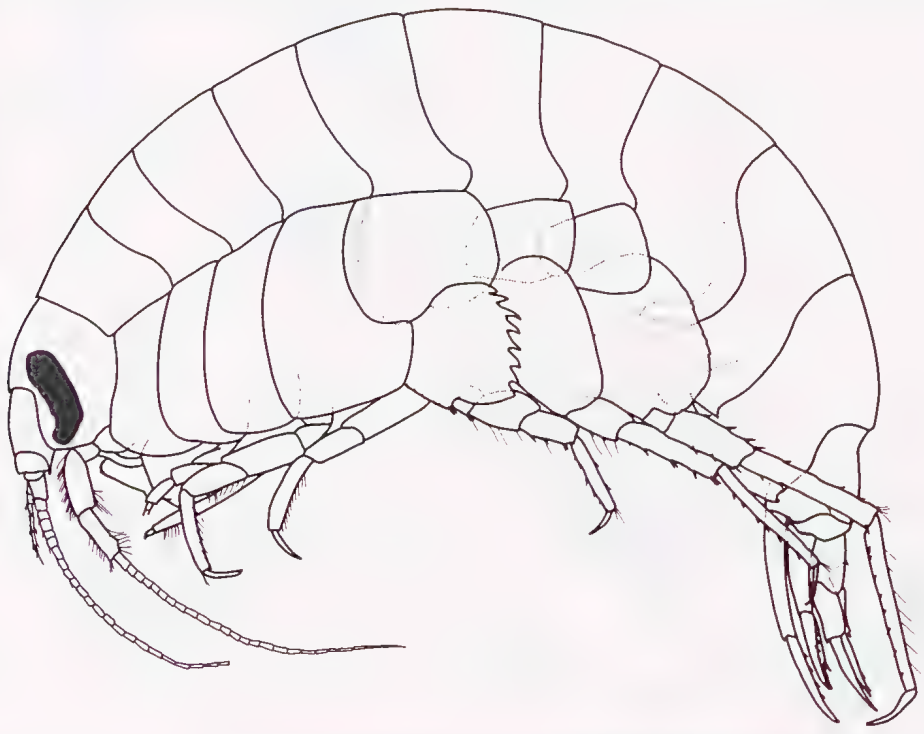

Fig.6. *Ichnopus capricornus* n.sp., paratype female, 10 mm, AM P39645, Heron Island, Great Barrier Reef, Australia.

Queensland, Australia, 23°26'S 151°55'E, baited trap, intertidal, on boulder ridge on north side of island, N.L. Bruce, 25 June 1979, QLD-85; 230 PARATYPES, AM P39646, 10 PARATYPES, BMNH 1990:33:10, 10 PARATYPES, USNM 253719, Heron Island, Queensland, 23°26'S 151°55'E, baited trap on beach rock, low tide level, A.J. Bruce, 12 June 1978, QLD-86.

Additional material examined. 156 specimens, AM P39585, patch reef between Lizard Island and Eagle Island, Queensland, 14°40'S 145°28'E, baited trap at night on sand with coral patches, 8 m, J.K. Lowry & R.T. Springthorpe, 4 Feb. 1987; 13 specimens, AM P39586, lagoon channel between beach and Bird Islet, Lizard Island, Queensland, baited trap at night on sand at base of coral outcrop, 13 m, J.K. Lowry & R.T. Springthorpe, 7 Feb. 1987; 10 specimens, AM P39675, North Point, Lizard Island, Queensland, baited trap at night on top of coral outcrop, 3 m, J.K. Lowry & R.T. Springthorpe, 9 Feb. 1987; 4 specimens, AM P39676, same data except baited trap at night on coral rubble near large coral outcrop, 8 m; 17 specimens, AM P39677, same data except baited trap on sand patches among coral, 12 m; 20 specimens, AM P39904, reef edge at lagoon channel, off Trawler Beach, Lizard Island, baited trap on sand and coral near large formations of yellow *Turbinaria reniformis* Bernard in 3-4 m, J.K. Lowry & R.T. Springthorpe, 15 Feb. 1987.

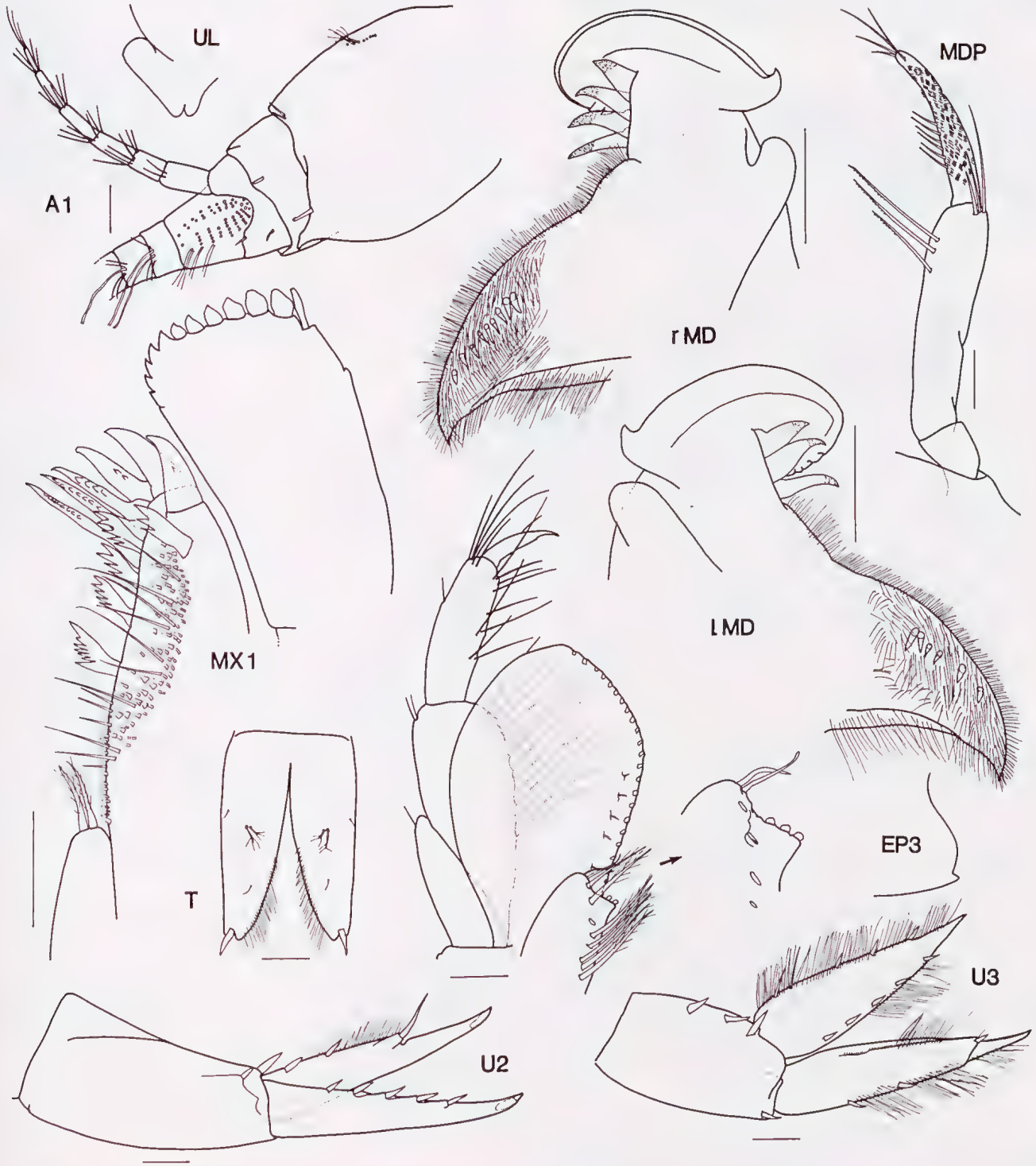

Fig.7. *Ichnopus capricornus* n.sp., holotype female, 10 mm, AM P39644, Heron Island, Great Barrier Reef, Australia. Scales represent 0.1 mm.

Diagnosis. Antenna 1: peduncular article 1 with long posteroventral tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli present in male only. Upper lip rounded. Mandible: left lacinia mobilis absent; accessory spine row, left with 3, right with 4 spines; molar setose, weakly spinose; palp article 2 slender. Maxilla 1 with ST7 multicuspidate distally; palp inner margin distally serrate. Maxilliped: inner plate with 3 nodular spines; palp article 2 broad. Gnathopod 1: ischium and carpus very long; dactylus with long cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin deeply serrate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with weak constriction.

Description. Based on holotype female, 10 mm and paratype male, 9.8 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, broadly rounded; rostrum absent; eyes reniform, enlarged in reproductive male. *Antenna 1:* medium length, about 0.3 times as long as body, 0.82 times as long as antenna 2; peduncular article 1 short, as long as broad, with long posterodistal tooth; accessory flagellum 6-articulate (male 7); callynophore, well-developed 2-field in female and male, with posterodistal setae; flagellum long, 26-articulate (male 30); calceoli present in male. *Antenna 2:* about 0.4 times as long as body in female; flagellum 26-articulate (male 34); peduncle with brush setae in female and male, peduncular articles 4 and 5 not swollen in female or male; calceoli present in male.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded. *Mandible:* incisors symmetrical, with slightly convex margins; left lacinia mobilis absent; accessory spine row, left with 3 spines, right with 4 spines; molar setose, sparsely spinose; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, slender, with 3 setae along distal third of medial margin, 3 setae on distolateral corner; article 3 slender, falcate, with 6 proximal D-setae and 4 short E-setae. *Maxilla 1:* inner plate small, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4

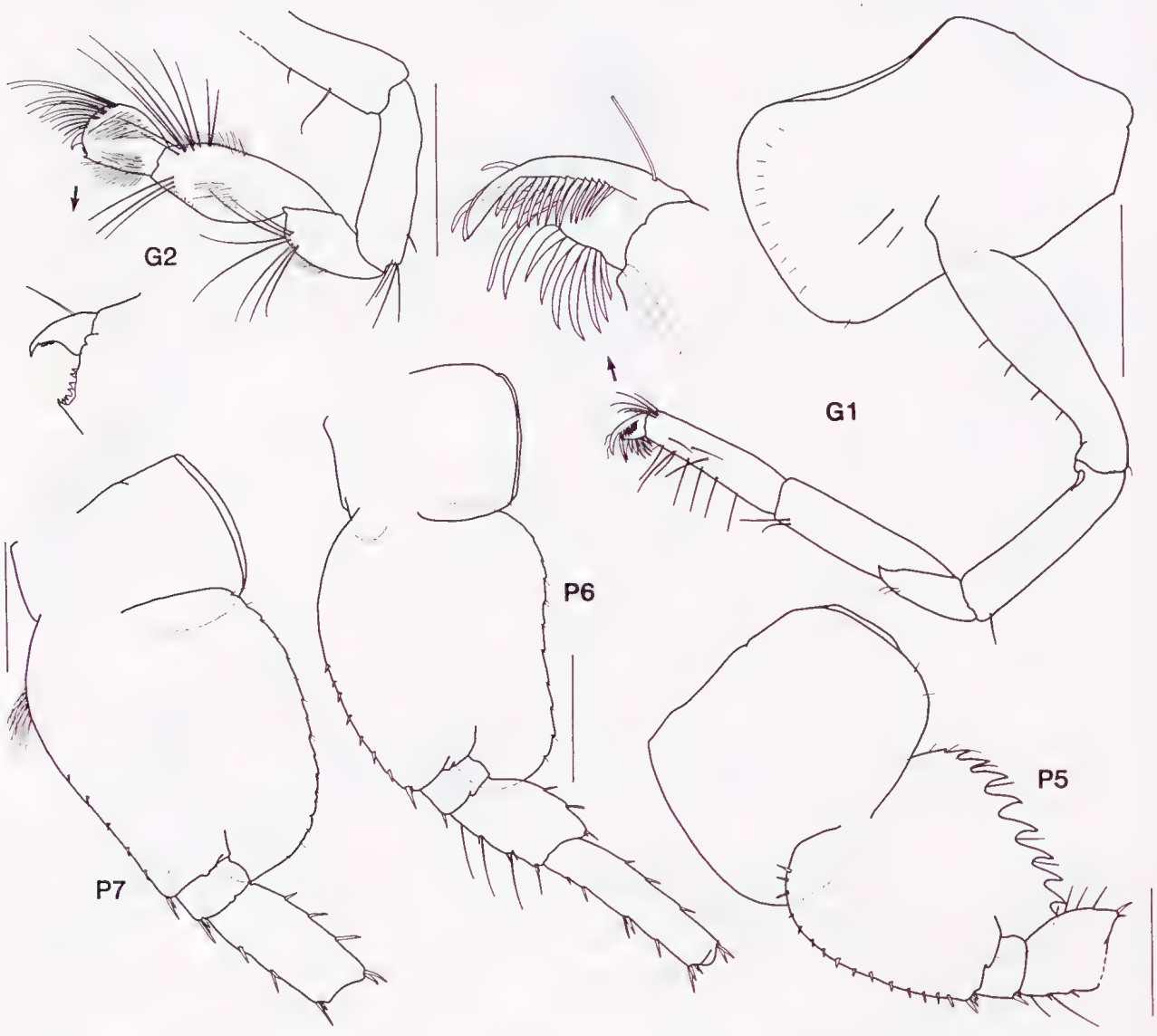

Fig.8. *Ichnopus capricornus* n.sp., holotype female, 10 mm, AM P39644, Heron Island, Great Barrier Reef, Australia. Scales represent 0.5 mm.

crown arrangement, ST1 to ST3 large, stout, weakly cuspidate, ST4 to ST6 large, slender, multicuspidate, ST7 short, multicuspidate distally, STA 2-cuspidate, STB to STD 3- to 4-cuspidate; palp large, 2-articulate, with 6 terminal spines and 1 flag seta. *Maxilla 2:* inner plate three quarters as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 3 well-developed nodular spines, oblique setal row reduced, with 8 plumose setae; outer plate medium size, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, submarginal setae vestigial; palp well developed, article 2 broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium very long, about 4.3 times as long as broad; carpus very long, 4 times as long as broad, 1.2 times as long as propodus; propodus long, subrectangular, 3.8 times as long as broad, margins subparallel; posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of about 13 medial spines and a row of 9 cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal in size to coxa 3; carpus long, 2.6 times as long as broad, posterior margin broadly lobate; propodus subovate, short, 1.3 times as long as broad; palm transverse, with slightly concave, serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe, anterior and posterior margins subparallel; male merus/carpus with plumose setae. *Peraeopod 5:* coxa equilobate; basis expanded with posterior margin deeply serrate. *Peraeopod 7:* basis, posterior margin slightly rounded with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with a small notch on posteroventral corner. *Uropod 1:* with long fine setae; rami subequal in length. *Uropod 2:* with long fine setae; rami subequal in length, inner ramus with weak constriction. *Uropod 3:* peduncle short, 1.76 times as long as broad, without lateral flange; rami lanceolate, subequal in length, with long fine setae and minutely serrate margins, plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (85%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. *Ichnopus capricornus* is a member of the *I. taurus* species group. It appears to be most closely related to *I. teretis*. They differ in the shape of peraeopod 7 basis and the posteroventral notch on epimeron 3. Both species have a weak constriction on the inner ramus of uropod 2.

Ichnopus capricornus is a tropical nocturnal scavenger which lives on shallow hard bottoms often covered with *Acropora* plates.

Etymology. The species takes its name from the Tropic of Capricorn.

Distribution. *Ichnopus capricornus* is known only from Heron Island and Lizard Island, Great Barrier Reef, Australia, in less than 30 m depth.

Ichnopus caritus n.sp.

Figs 9-10

Type material. HOLOTYPE, female, ovigerous (7 eggs), 10 mm, AM P39652, 13 PARATYPES, AM P39653, off Possession Point, King George Sound, Western Australia, 35°02.5'S 117°55'E, sand and detritus from bases of seagrasses, 10 m, R.T. Springthorpe & J.K. Lowry, 14 Dec. 1983, WA-131.

Additional material examined. One specimen, NMV J19736, 23 km east of Cape Rochon, Three Hummock Island, Tasmania, 40°22.2'S 145°17'E, sand, 40 m, M. Gomon & G.C.B. Poore on FRV *Sarda*, 3 Nov. 1980, cruise 80-Sa-1, stn BSS-112; 3 specimens, AM P39654, 25 km north-east of Deal Island, Tasmania, eastern Bass Strait, 39°16.8'S 147°33.2'E, sand, 57 m, epibenthic sled, R. Wilson on RV *Tangaroa*, 18 Nov. 1981, cruise 81-T-1, stn BSS-174S; 1 specimen, NMV J19737, same data except 39°16.8'S 147°33.2'E, grab, stn BSS-174G; 1 specimen, NMV J19738, 15 km east of Cape Wellington, Wilsons Promontory, Victoria, eastern Bass Strait, 39°03.2'S 146°39.5'E, muddy fine sand, 55 m, epibenthic sled, R. Wilson on RV *Tangaroa*, 18 Nov. 1981, cruise 81-T-1, stn BSS-179S; 10 specimens, NMV J19739, 8 km south of South East Point, Wilsons Promontory, Victoria, central Bass Strait, 39°12.9'S 146°27.3'E, medium sand, 65 m, epibenthic sled, R. Wilson on RV *Tangaroa*, 18 Nov. 1981, cruise 81-T-1, stn BSS-180S; 3 specimens, NMV J19740, 26 km south-east of Aireys Inlet, Victoria, central Bass Strait, 38°39.8'S 144°18.2'E, very fine sand, 79 m, R. Wilson on RV *Tangaroa*, 19 Nov. 1981, cruise 81-T-1, stn BSS-181S; 2 specimens, NMV J19741, 40 km south-south-west of Lakes Entrance, Victoria, 38°18.0'S 147°37.0'E, muddy fine shell, 55 m, epibenthic sled, M. Gomon & R. Wilson on FV *Silver Gull*, 31 July 1983, cruise 83-SG-1, stn BSS-209S.

Diagnosis. Antenna 1: peduncular article 1 with long posteroventral tooth; callynophore with posterodistal spines. Antennae 1 and 2: calceoli in male only. Upper lip rounded. Mandible: left lacinia mobilis absent; accessory spine row, left with 3, right with 4 spines; molar setose, without spines; palp article 2 slender. Maxilla 1 with ST7 multicuspidate distally; palp inner margin distally serrate. Maxilliped: inner plate with 3 nodular spines; palp article 2 very broad. Gnathopod 1: ischium and carpus very long; dactylus with long cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin deeply serrate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with moderate constriction.

Description. Based on holotype female, 10 mm, and paratype male, 6 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, broadly rounded; rostrum absent; eyes reniform, slightly enlarged in

reproductive male. *Antenna 1:* medium length, 0.3 times as long as body, subequal in length to antenna 2; peduncular article 1 short, about as long as broad, with long posterodistal tooth; accessory flagellum 8-articulate (male 6); callynophore, well-developed 2-field in female and male with 2 large posterodistal spines; flagellum

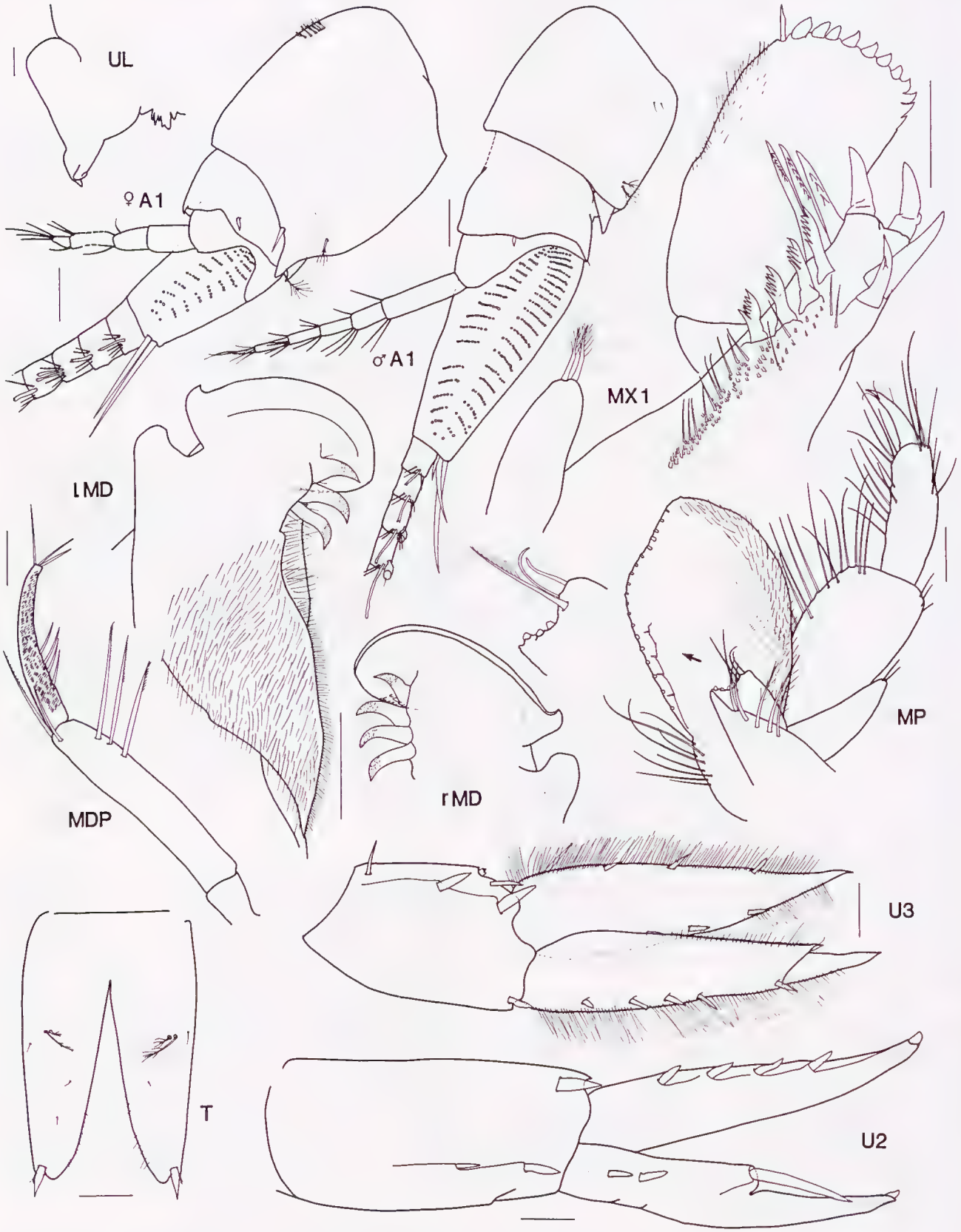

Fig.9. *Ichnopus caritus* n.sp., holotype female, 10 mm, AM P39652, paratype male, 6 mm, AM P39653, off Possession Point, King George Sound, Western Australia. Scales represent 0.1 mm.

long, 24-articulate (male 14); calceoli present in male. *Antenna 2:* about 0.3 times as long as body in female; flagellum 26-articulate (male 16-articulate); peduncle with brush setae in female and male, peduncular articles 4 and 5 not swollen in female or male; calceoli present in male.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded. *Mandible:* incisors symmetrical with slightly convex margins; left lacinia mobilis absent; accessory spine row, left with 3 spines, right with 4 spines; molar setose, without spines; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, slender, with 3 setae along distal third of medial margin, 2 setae on distolateral corner; article 3 slender, falcate, with 4 proximal D-setae and 3 short E-setae. *Maxilla 1:* inner plate small, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement,

Fig.10. *Ichnopus caritus* n.sp., holotype female, 10 mm, AM P39652, off Possession Point, King George Sound, Western Australia. Scales represent 0.5 mm.

ST1 to ST3 large, stout, without cusps, ST4 to ST6 large, slender, multicuspidate, ST7 short, multicuspidate distally, STA 1-cuspidate, STB to STD 4- to 5-cuspidate; palp large, 2-articulate, with 7 terminal spines and 1 flag seta. *Maxilla 2:* inner plate three quarters as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 3 well-developed nodular spines, oblique setal row reduced, with 6-7 plumose setae; outer plate medium size, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, 4 vestigial submarginal setae present; palp well developed, article 2 very broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium very long, about 4.1 times as long as broad; carpus very long, 4.0 times as long as broad, 1.4 times as long as propodus; propodus long, subrectangular, 3 times as long as broad, margins subparallel; posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of 18 medial spines and a row of 10 cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal in size to coxa 3; carpus long, 2.6 times as long as broad, posterior margin broadly lobate; propodus subovate, short, 1.3 times as long as broad; palm transverse, with straight, slightly serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe, anterior and posterior margins subparallel; male merus/carpus without plumose setae (possibly immature). *Peraeopod 5:* coxa bilobate, anterior margin slightly produced ventrally; basis expanded with posterior margin deeply serrate. *Peraeopod 7:* basis, posterior margin slightly rounded with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with small notch on posteroventral corner. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: with long fine setae; rami subequal in length, inner ramus with moderate constriction. *Uropod 3:* peduncle short, 1.6 times as long as broad, without lateral flange; rami lanceolate, subequal in length, with long fine setae and minutely serrate margins, plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (75%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. *Ichnopus caritus* is a member of the *I. taurus* species group. It is the sister taxon of a group of Australian species which have moderately spinose molars. It has no spines on the mandibular molar. *Ichnopus caritus* and *I. parriwi* both have three accessory spines on the left mandible, but *I. parriwi* has calceoli in the male and female. *Ichnopus caritus* and *I. cribensis* differ only in the spination of the molar and the spination of the accessory spine row. *Ichnopus tenuicornis* has spines on the molar and an enlarged palm on female gnathopod 2.

Etymology. The latin word *caritus* means 'lacking or devoid of', in reference to the complete absence of spines on the mandibular molar.

Distribution. *Ichnopus caritus* is known along the south coast of Australia from Albany to Bass Strait in 10 to 79 m depth.

Ichnopus comorensis n.sp.

Figs 11-12

Ichnopus spinicornis.–Ledoyer, 1986: 764, fig.297.

Type material. HOLOTYPE, sex not known, 5 mm, MNHN Am 4150, south of South Reef, Ile de Mayotte, Comores Archipelago, Indian Ocean, 13°05.2'S 45°07.9'E, beige organogenic sand with much debris and madreporites, 400-520 m, dredged, 27 Mar. 1977, Mission Benthedi, stn DS 42.

Diagnosis. Antenna 1: peduncular article 1 with short posteroventral tooth; callynophore with 1 small posterodistal seta. Antennae 1 and 2: calceoli present. Upper lip rounded. Mandible: left lacinia mobilis present; accessory spine row, left with 4, right with 3 spines; molar setose, without spines; palp article 2 slightly broadened distally. Maxilla 1 with ST7 multicuspidate medially; palp inner margin distally smooth. Maxilliped, inner plate with 2 nodular spines; palp article 2 broad. Gnathopod 1: ischium and carpus long; dactylus with short cuticular spines. Gnathopod 2: palm minute. Peraeopod 5: basis with posterior margin minutely crenate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with strong constriction.

Description. Based on holotype (sex not known), 5 mm, MNHN Am 4150. *Head*: deeper than long; lateral cephalic lobe well developed, narrowly rounded; rostrum absent; eyes reniform. *Antenna 1*: medium length; peduncular article 1 short, 1.2 times as long as broad, with short posterodistal tooth; accessory flagellum short, 5-articulate, article 1 at least twice as long as article 2; flagellum of medium length, 13-articulate; callynophore weakly developed 2-field, with 1 small posterodistal seta; calceoli present. *Antenna 2*: peduncle without brush setae; peduncular articles 4 and 5 not enlarged; flagellum 13-articulate; calceoli present.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, profile not known. *Mandible*: incisors symmetrical, large, both with slightly convex margins; left lacinia mobilis a spine; accessory spine row, left with 4, right with 3 short, slender, simple spines, without intermediate setae; molar a setose tongue; mandibular palp attached midway, article 1 short, about as long as broad, without setae; article 2 elongate, slightly broadened distally, 4.2 times as long as broad, 1.4 times as long as article 3, without setae on medial surface, with 2 setae on distal third of medial margin, 1 seta

on distolateral corner; article 3 slender, falcate, long, 4.6 times as long as broad, with 2 proximal D-setae and 4 apical E-setae. *Maxilla 1*: inner plate not known; outer plate extremely narrow with 11 spine-teeth in 7/4 crown arrangement; ST1 to ST3 large, stout, weakly cuspidate, ST4 large, stout, 4-cuspidate, ST5 large, slender, 5-cuspidate, ST6 large, multicuspidate, ST7 short, multicuspidate medially; STA large, slightly displaced from STB-STD, 3-cuspidate, STB long, broad, 4-cuspidate, STC long, broad, 5-cuspidate, STD small, 6-cuspidate; palp large, 2-articulate, with 3 terminal spines, flag seta present on distolateral corner, distomedial margin smooth. *Maxilla 2*: not known. *Maxilliped*: inner plate large, subrectangular, with 2 well-developed nodular spines, oblique setal row reduced with 1 simple seta; outer plate small, subovate, apical setae and spines absent, medial spines present, bead-shaped, submarginal setae vestigial; palp well developed, 4-articulate, article 2 broad, 1.9 times as long as broad, 1.3 times as long as article 3; article 3 long, slender, 2.3 times as long as broad; dactylus well developed, with 1 subterminal seta, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner, posterior margin straight; basis long, slender, 2.9 times as long as broad, without setae along anterior margin; ischium long, 2.3 times as long as broad; carpus subtriangular, long, 2.1 times as long as broad, 1.25 times as long as propodus; propodus large, subtriangular, 2.2 times as long as broad, margins tapering distally, posterior margin smooth, straight, without spines; palm absent; dactylus complex, with large subterminal tooth, a row of 4 medial spines and a row of 6 short cuticular teeth along posterior margin. *Gnathopod 2*: minutely subchelate; coxa large, subequal in size to coxa 3; ischium long, 3.5 times as long as broad; carpus long, 2.7 times as long as broad, posterior margin broadly lobate; propodus subquadrate, short, 1.6 times as long as broad; palm acute, with concave, smooth margin, posterodistal corner without spines.

Peraeopod 4: coxa with well-developed posteroventral lobe, anterior and posterior margins subparallel; merus-carpus without plumose setae; propodus with 3 setae and 1 pair of distal spines along posterior margin; dactylus long, slender. *Peraeopod 5*: coxa equilobate; basis expanded with posterior margin minutely crenate; merus slightly expanded posteriorly. *Peraeopod 6*: coxa small, not lobate posteriorly; basis expanded posteriorly with minutely crenate posterior

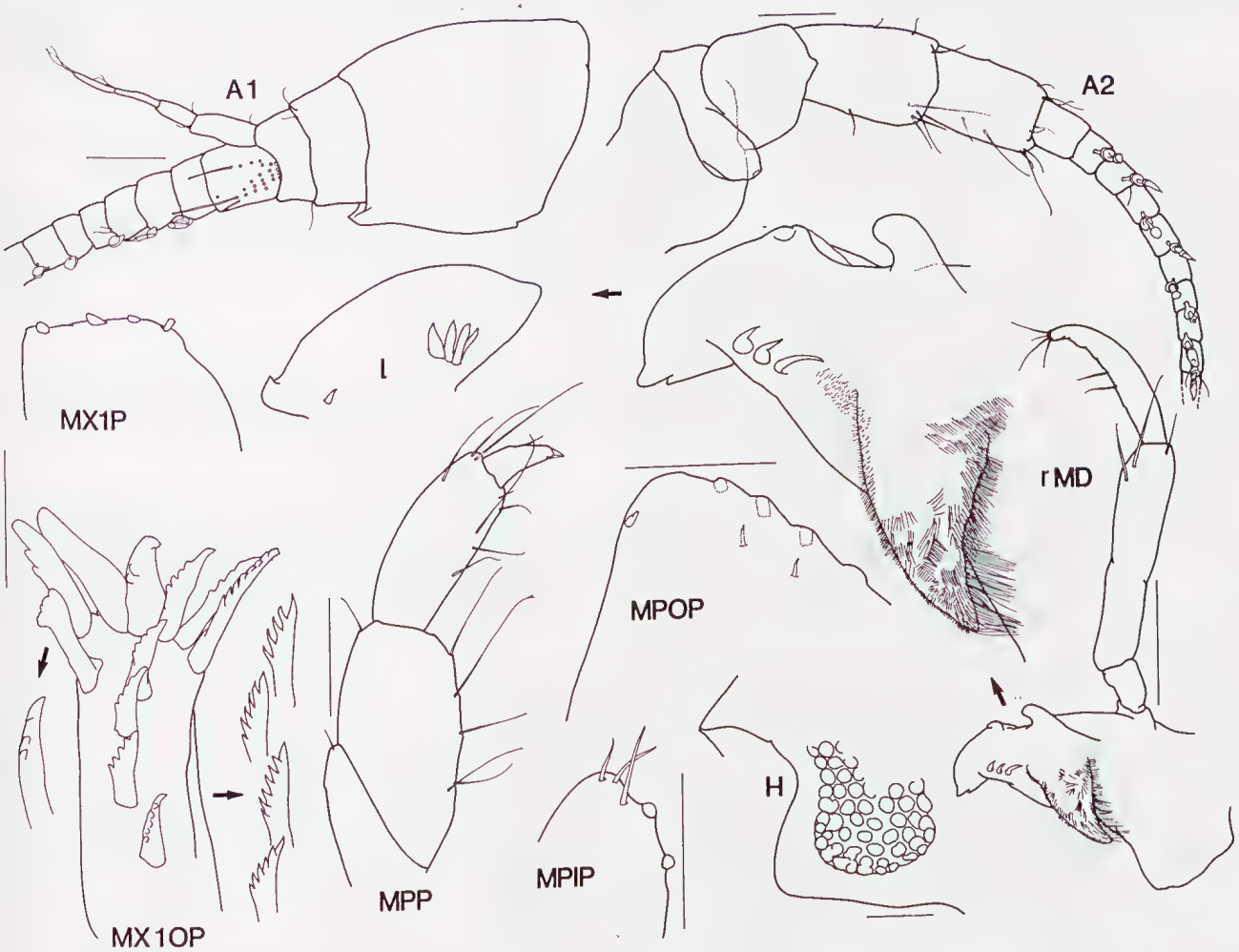

Fig.11. *Ichnopus comorensis* n.sp., holotype, sex not known, 5 mm, MNHN Am 4150, off Mayotte Island, Comores Archipelago, western Indian Ocean. Scales for MX1OP, MX1P, MPIP, MPOP represent 0.5 mm; remainder represent 0.1 mm.

margin; merus slightly expanded posteriorly. *Peraeopod 7*: basis expanded posteriorly, posterior margin almost straight, minutely crenate, posteroventral corner subquadrate, posteroventral margin rounded; merus not expanded posteriorly; propodus with 3 spines along anterior margin and 2 setae along posterior margin;

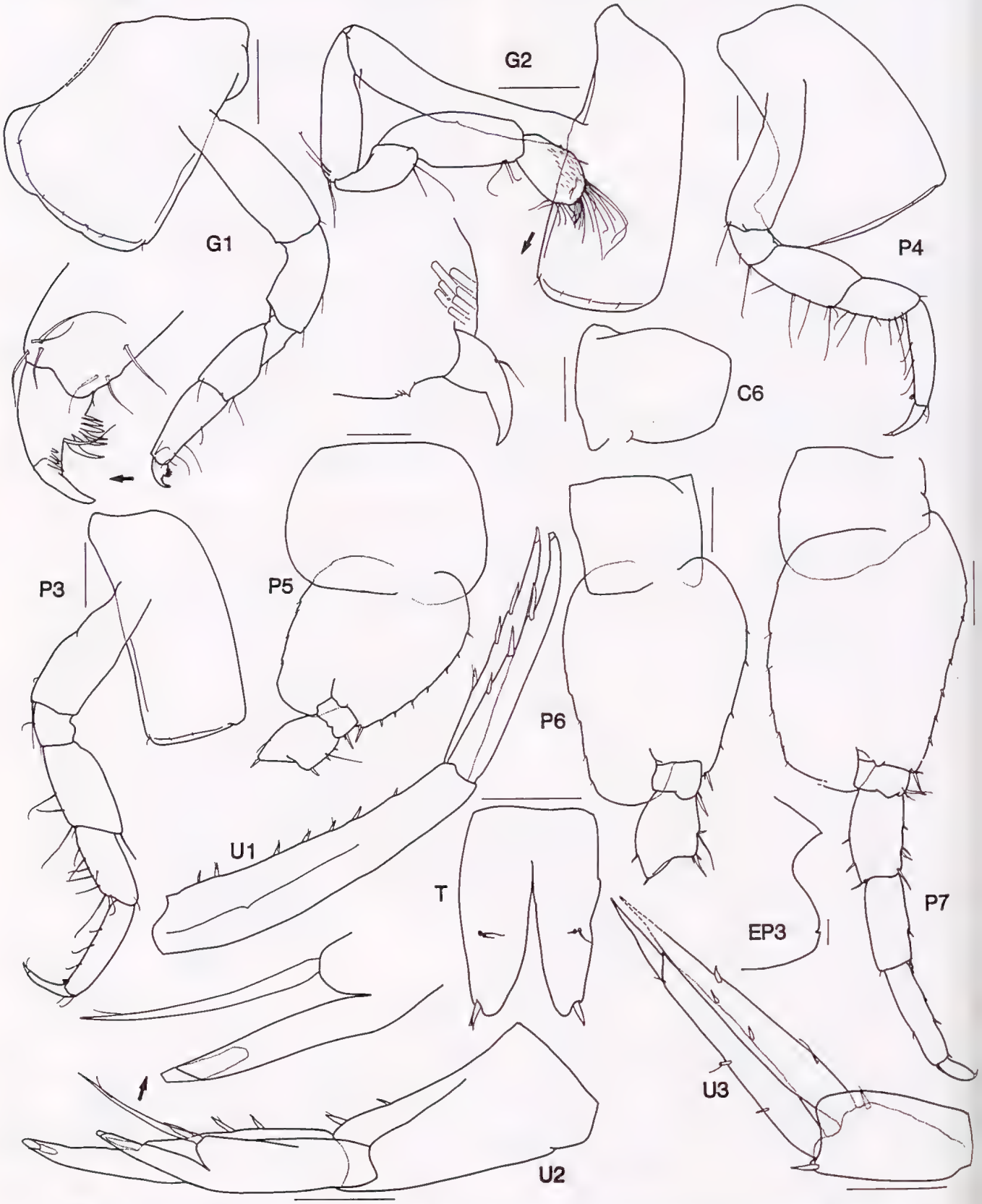

Fig.12. *Ichnopus comorensis* n.sp., holotype, sex not known, 5 mm, MNHN Am 4150, off Mayotte Island, Comores Archipelago, western Indian Ocean. Scales for G1-2, P3-4 represent 0.2 mm; remainder represent 0.1 mm.

dactylus short, stocky.

Oostegites: not known. *Gills*: not known.

Epimeron 3: posteroventral corner with small notch. *Uropod 1*: without fine setae; peduncle with 7 dorsolateral spines; rami subequal in length; outer and inner rami each with 3 spines. *Uropod 2*: without fine setae; with 1 dorsolateral and 1 distolateral spines, with 1 dorsomedial and 1 distomedial spines; outer ramus slightly longer than inner ramus; outer ramus with 3 spines, inner ramus with 1 long spine above strong constriction. *Uropod 3*: peduncle long, 2.2 times as long as broad, with 1 distolateral spine; rami lanceolate, subequal in length; outer ramus 2-articulate, article 2 short, with 2 lateral spines, inner ramus with 2 medial and 1 lateral spines; plumose setae absent. *Telson*: 1.5 times as long as broad, deeply cleft (71%), without dorsal spines, distal margins rounded, with 1 pair of emarginate spines.

Remarks. This species was originally reported by Ledoyer (1986) as *Ichnopus spinicornis*. Although the two species are closely related *I. comorensis* differs from *I. spinicornis* as follows: significantly fewer articles in the accessory flagellum and the antennal flagella; significantly fewer D-setae on mandibular palp article 3; smoother posterior margin on the basis of peraeopod 5; significantly fewer spines on the outer ramus of uropod 2; a much smaller notch on epimeron 3.

Etymology. Named after the Comores Archipelago where the species was first discovered.

Distribution. Off Mayotte Island, Comores Archipelago, south-western Indian Ocean, in 400 to 520 m depth.

Ichnopus cribensis n.sp.

Figs 13-14

Type material. HOLOTYPE, female, 11 mm, NMV J19735, 2 PARATYPES, male, 16.5 mm, juvenile, 5.5 mm, NMV J3640, Crib Point, Western Port, Victoria, Australia, 38°21'S 145°14'E, 5 m, Smith-McIntyre grab, Marine Studies Group, Victorian Fisheries & Wildlife Department, 14 July 1964, Crib Point Benthic Survey, stn CPBS A1.

Additional material examined. 112 specimens, NMV J13736, NMV J3641 to NMV J3685 and AM P39673, from 26 stations, Crib Point, Western Port, Victoria, Australia, 38°20-21'S 145°13-15'E, 2-19 m, Smith-McIntyre grab, Marine Studies Group, Victorian Fisheries & Wildlife Department, Feb.-Mar. 1965, Crib Point Benthic Survey; 10 specimens, NMV J3686 to J3688, from 3 stations, Western Port, Victoria, 38°16-25'S 145°18-24'E, sand, 10-14 m, Marine Studies Group, Jan.-Nov. 1973, Westernport Bay Environmental Study; 1 specimen, NMV J3337, Western Port, Victoria, A.O. Sayce collection; 1 male, NMV J19734, 32 km north-west of Devonport, Tasmania, 40°49.8'S 146°31.3'E to 40°48.2'S 146°33.7'E, mud, 68-70 m, otter trawl, M.F. Gomon, G.C.B. Poore & C.C. Lu on FRV *Hai Kung*, 4 Feb. 1981, Bass Strait Survey stn BSS-134T; 2 specimens, AM P41005, 200 m off small shingle beach, north end of Tower Bay, D'Entrecasteaux Channel, Tasmania, 43°23.6'S 147°01.7'E, baited trap, 30 m, J.K. Lowry & S.J. Keable on the *Flying Scud*, 20-21 Apr. 1991, TAS-220; 6 specimens, AM P41006, 300 m off small shingle beach, north end of Tower Bay, D'Entrecasteaux Channel, Tasmania, 43°23.6'S 147°2.1'E, baited trap, 40 m, J.K. Lowry & S.J. Keable on the *Flying Scud*, 20-21 Apr. 1991, TAS-221; 12 specimens, AM P41007, 400 m off small shingle beach, north end of Tower Bay, D'Entrecasteaux Channel, Tasmania, 43°23.6'S 147°2.4'E, baited trap, 40 m, J.K. Lowry & S.J. Keable on the *Flying Scud*, 20-21 Apr. 1991, TAS-222; 1 immature female, AM P39674, Blanche Harbour, Spencer Gulf, South Australia, 32°42'S 137°46'E, 9 m, K. Sheard on FL *Whyalla*, 8 March 1938; 1 female, AM P18152, east of Bald Island, south-east Western Australia, 34°55'S 119°00'E, 76 m, benthic grab, R.J. MacIntyre for CSIRO on HMAS *Gascoyne*, 7 Aug. 1962, stn G3/150/62, sample 2B.

Diagnosis. Antenna 1: peduncular article 1 with long posterodistal tooth; callynophore with posterodistal spines. Antennae 1 and 2: calceoli in male only. Upper lip rounded. Mandible: left lacinia mobilis absent; accessory spine row, left and right each with 4 spines; molar setose, weakly spinose; palp article 2 slender. Maxilla 1 with ST7 multicuspidate distally; palp inner margin distally serrate. Maxilliped: inner plate with 3 nodular spines; palp article 2 very broad. Gnathopod 1: ischium and carpus very long; dactylus with long cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin deeply serrate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with moderate constriction.

Description. Based on holotype female, 11 mm and paratype male, 16.5 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, broadly rounded; rostrum absent; eyes reniform, slightly enlarged in reproductive male. *Antenna 1*: medium length, about 0.25 times as long as body, 0.8 times as long as antenna 2; peduncular article 1 short, about as long as broad, with long posterodistal tooth; accessory flagellum 7-articulate (male 9), article 1 elongate; callynophore, well-developed 2-field in female and male with 4-5 large posterodistal spines; flagellum long, 20-articulate (male 30); calceoli present in male. *Antenna 2:* about 0.3 times as long as body in female; flagellum 26-articulate, 0.4 times as long as body in male (54-articulate); peduncle with brush setae in female and male (not present in juvenile), peduncular articles 4 and 5 not swollen in female or male; calceoli present in male.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded. *Mandible:* incisors symmetrical with slightly convex margins; left lacinia mobilis absent; accessory spine row, left and right with 4 spines; molar setose, weakly spinose; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, slender, with 4 setae along distal third of medial margin, (male slightly expanded distally with 9 setae), 2 (male 4) setae on distolateral

corner; article 3 slender, falcate, with 8 (male 12) proximal D-setae and 3 (male 4) short E-setae. *Maxilla 1:* inner plate short, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, without cusps, ST4 to ST6 large, slender, multicuspidate, ST7

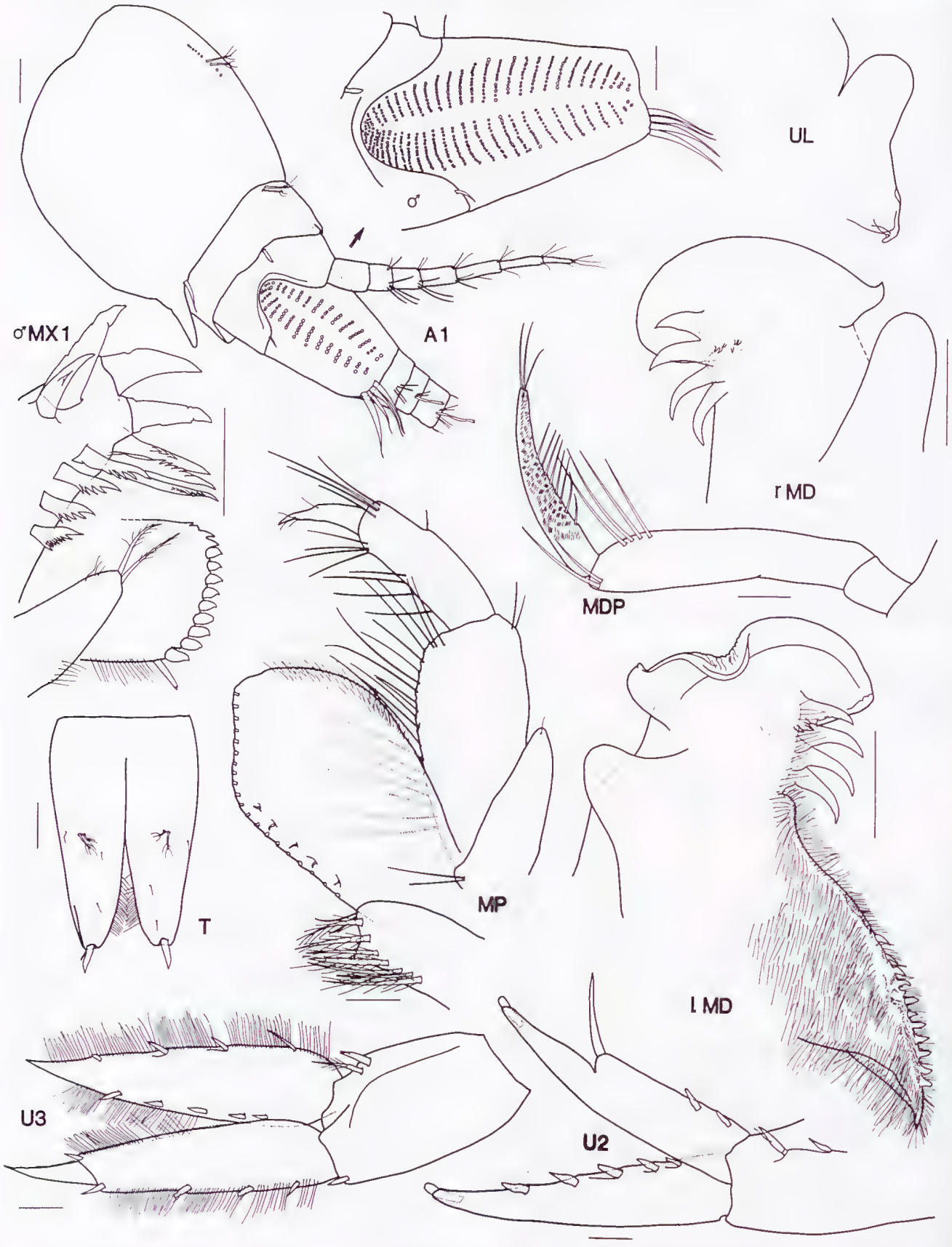

Fig.13. *Ichnopus cribensis* n.sp., holotype female, 11 mm, NMV J19735, paratype male, 16.5 mm, NMV J3640, Western Port, Victoria, Australia. Scales represent 0.1 mm.

short, multicuspidate distally, STA 1-cuspidate, STB to STD 4-cuspidate; palp large, 2-articulate, with 9 terminal spines and 1 flag seta. *Maxilla 2:* inner plate three quarters as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 3 well-developed nodular spines, oblique setal row reduced, with 7 plumose setae; outer plate medium size, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, 5 vestigial submarginal setae present; palp well developed, article 2 very broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium very long, about 4.2 times as long as broad; carpus very long, 4.2 times as long as broad, 1.3 times as long as propodus; propodus long, subrectangular, 3 times as long as broad, margins subparallel, posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of 19 medial spines and a row of 10 long cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal in size to coxa 3; carpus long, 2.75 times as long as broad, posterior margin broadly lobate; propodus subquadrate, short, 1.5 times as long as broad; palm transverse, with straight, slightly serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe; male merus/carpus with plumose setae. *Peraeopod 5:* coxa bilobate, anterior margin slightly produced ventrally; basis expanded with posterior margin deeply serrate. *Peraeopod 7:* basis, posterior margin slightly rounded with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with small notch on posteroventral corner. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: with long fine setae; rami subequal

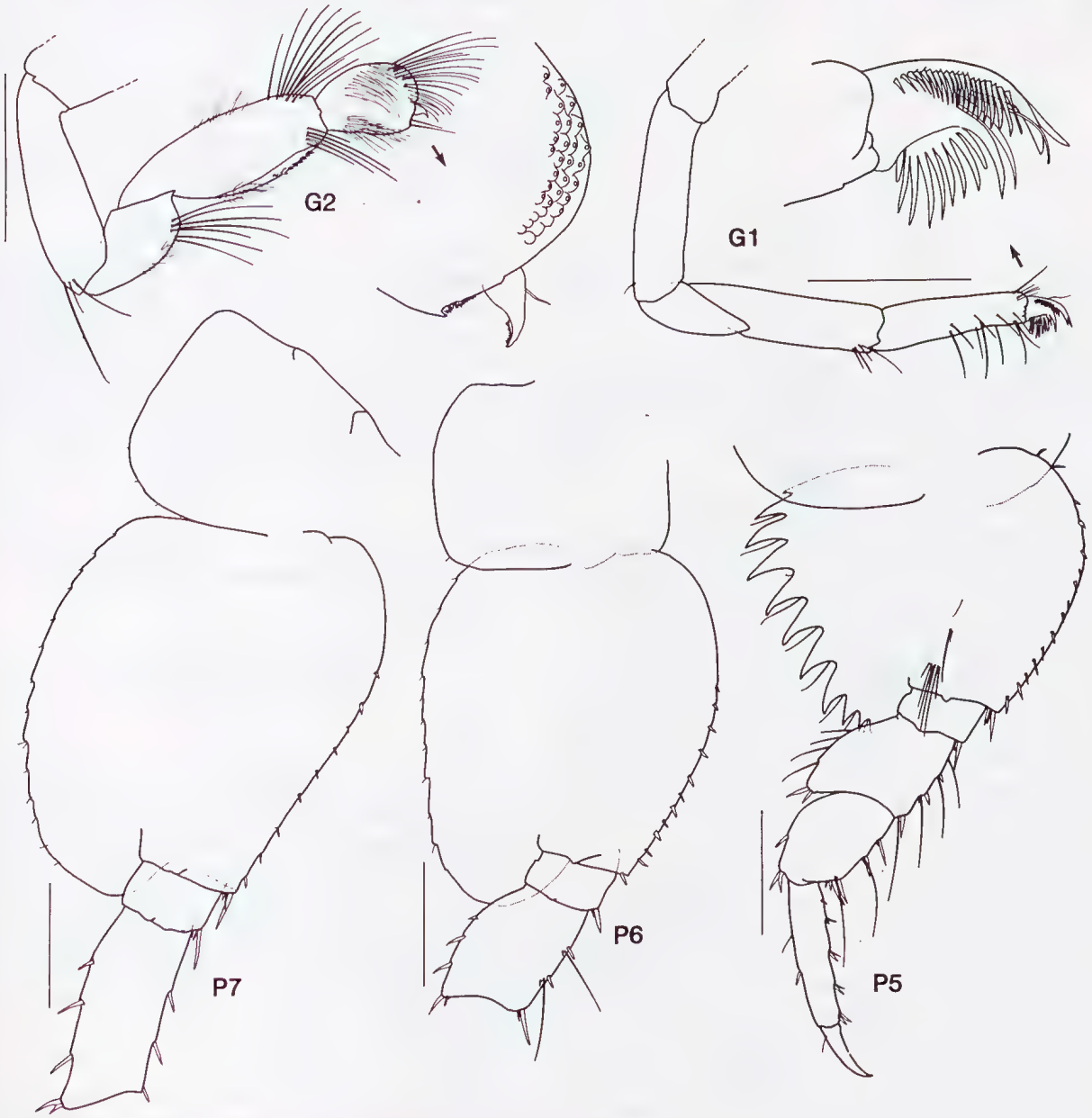

Fig.14. *Ichnopus cribensis* n.sp., holotype female, 11 mm, NMV J19735, Western Port, Victoria, Australia. Scales represent 0.5 mm.

in length, inner ramus with moderate constriction. *Uropod 3:* peduncle short, 1.75 times as long as broad, without lateral flange; rami lanceolate, subequal in length, with long fine setae and minutely serrate margins, plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (82%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. The relationship of *I. cribensis* to its sibling, *I. caritus*, has been discussed under that species.

Etymology. Named after Crib Point, the type locality.

Distribution. *Ichnopus cribensis* is known from Western Port in Victoria, off Devonport and in the D'Entrecasteaux Channel, Tasmania, Spencer Gulf in South Australia and east of Bald Island, south-east Western Australia, in 5 to 76 m depth.

Ichnopus macrobetomma Stebbing

Ichnopus macrobetomma Stebbing, 1917: 38, pl.96.

Type material examined. HOLOTYPE, ?male, SAM A19391, off East London, south-eastern South Africa, 33°09.5'S 28°03'E, 86 m.

All that remains of the type material is one slide which contains gnathopods 1 and 2, and peraeopods 3, 4, 6 and 7. The species cannot be fully redescribed and should be considered dubious until new material can be collected and studied. The type specimen is assumed to be a male, because of the very large eyes.

Partial description. Based on holotype ?male. *Head*: slightly deeper than long, lateral cephalic lobe well developed, broadly rounded; rostrum absent; eyes reniform, greatly enlarged in reproductive male. *Antenna 1:* medium length, about 0.3 times as long as body, 0.8 times as long as antenna 2; peduncular article 1 short, slightly longer than deep, with short posterodistal tooth; accessory flagellum 10-articulate; callynophore, well-developed 2-field in male; flagellum long, about 40-articulate. *Antenna 2:* about 0.4 times as long as body in male; peduncle with brush setae in reproductive male, peduncular articles 4 and 5 not swollen.

Mouthpart bundle: subquadrate. *Mandible:* left incisor with slightly convex margin; accessory spine row with 3 spines; molar setose with spines; mandibular palp attached midway; article 1 about twice as long as broad; article 2 elongate, slightly widened distally, with about 7 setae along distal third of medial margin, 1-2 setae on distolateral corner; article 3 slender, falcate, with about 9 proximal D-setae and short E-setae. *Maxilliped:* inner plate large, subrectangular; outer plate medium size, subovate, apical setae and spines absent; palp well developed, article 2 broad, dactylus well developed.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium very long 3.5 times as long as broad; carpus very long, 4.0 times as long as broad, about 1.3 times as long as propodus; propodus very long, subrectangular, about 3.3 times as long as broad, margins subparallel; posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of about 20 medial spines and a row of about 10 cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal in size to coxa 3; carpus long, 2.2 times as long as broad, posterior margin broadly lobate; propodus subrectangular, short, 1.8 times as long as broad; palm transverse, with convex margin.

Peraeopod 4: coxa with well-developed posteroventral lobe, male merus/carpus with plumose setae. *Peraeopod 5:* coxa bilobate; basis expanded with posterior margin minutely crenate. *Peraeopod 7:* basis, posterior margin slightly rounded, with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with a notched posteroventral corner. *Uropod 3:* rami lanceolate, subequal in length; plumose setae absent in male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (81%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. From our limited information, *I. macrobetomma* belongs in the *I. taurus* species group. It appears to be most closely related to *I. taurus* and has been placed in synonymy with it by Griffiths (1974: 309). However, it should remain separate until new material is collected and studied. It appears to differ from *Ichnopus* sp. of Walker, 1904, in having a slight posterodistal tooth, more articles in the accessory flagellum and more D-setae on article 3 of the mandibular palp.

Distribution. South-eastern Africa, 86 m.

Ichnopus malpatun n.sp.

Figs 15-16

Type material. HOLOTYPE, male, 10.5 mm, AM P41009, face of outer barrier between Rasch Pass and Wongat Island, Madang Lagoon, Papua New Guinea, 5°08.7'S 145°49.7'E, baited trap on coarse sand bottom next to vertical face of ?*Montipora* coral and sponges, 95 m, J.K. Lowry & J. Mizeu, 31 Jan.-1 Feb. 1990, JKL/PNG-120; PARATYPE, female, 10 mm, non-ovigerous, setose oostegites, MNHN Am 4401, Grand Passage, New Caledonia, 19°07.6'S 163°22.7'E, Waren Dredge, 165 m, RV *Vauban*, 14 Sept. 1985, MUSORSTOM IV, stn 0149.

Diagnosis. Antenna 1: peduncular article 1 with long posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli present in male and female. Upper lip rounded. Mandible: left lacinia mobilis absent;

accessory spine row, left and right each with 4 spines; molar setose, strongly spinose; palp article 2 strongly broadened distally. Maxilla 1 with ST7 multicuspidate medially; palp inner margin distally serrate. Maxilliped: inner plate with 2-3 nodular spines; palp article 2 broad. Gnathopod 1: ischium and carpus long; dactylus with short cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin deeply serrate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with moderate constriction.

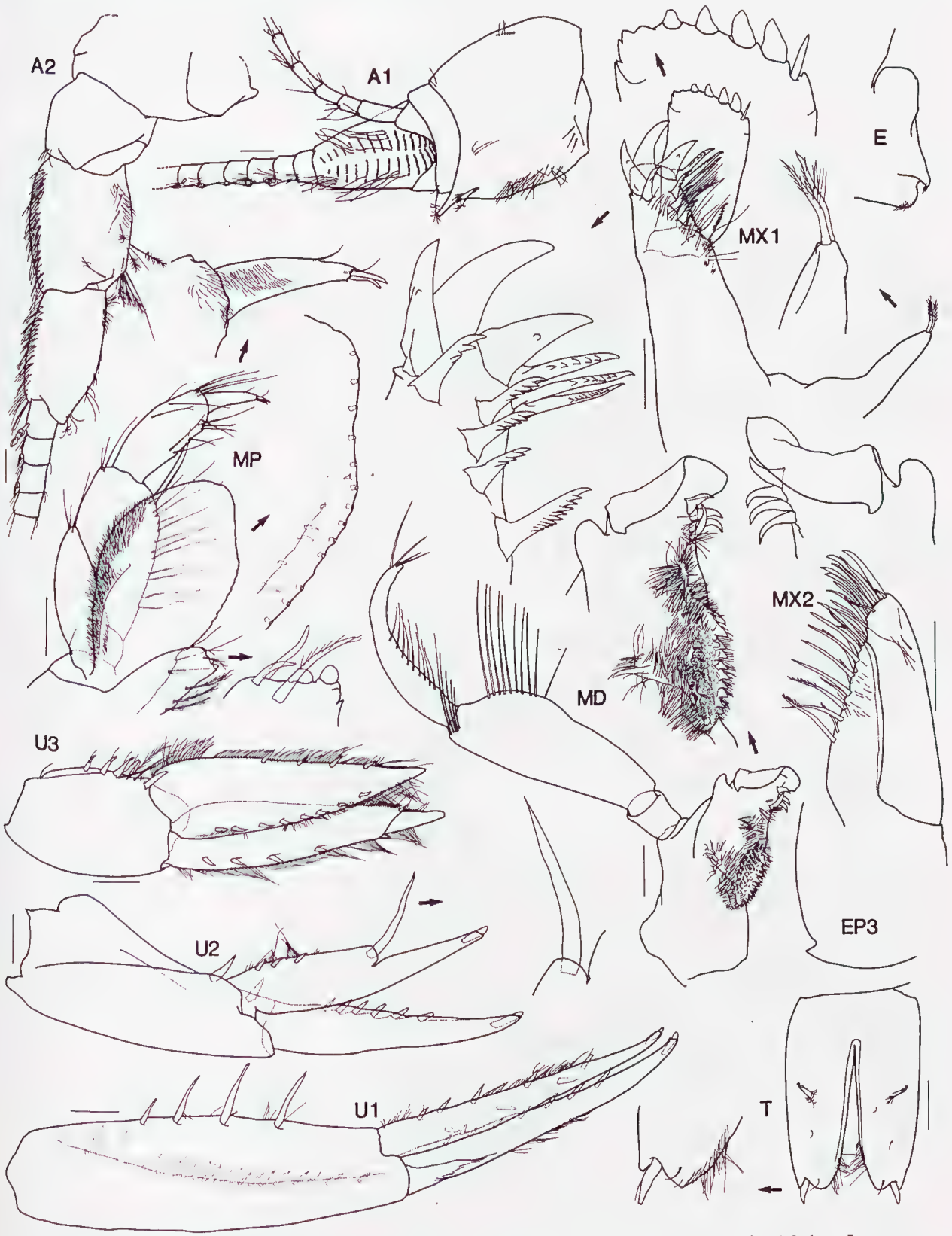

Fig.15. *Ichnopus malpatun* n.sp., holotype male, 10.5 mm, AM P41009, face of outer barrier, Madang Lagoon, Papua New Guinea. Scales represent 0.1 mm.

Description. Based on holotype male, 10.5 mm and paratype female, 10 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, narrowly rounded; rostrum absent; eyes reniform, slightly enlarged in reproductive male. *Antenna 1:* medium length, about 0.3 times as long as body, 0.5 times as

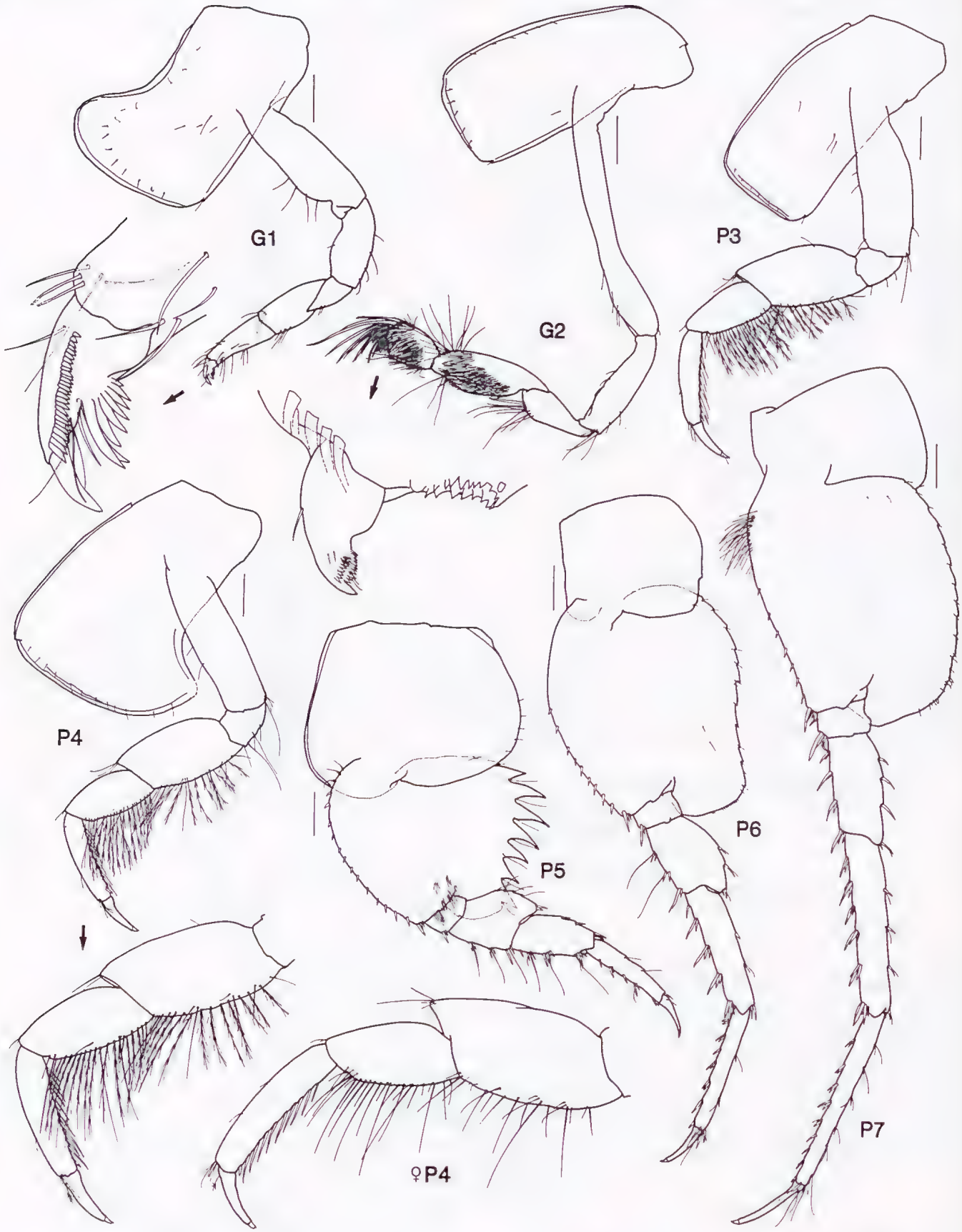

Fig.16. *Ichnopus malpatun* n.sp., holotype male, 10.5 mm, AM P41009, face of outer barrier, Madang Lagoon, Papua New Guinea. Paratype female, 10 mm, MNHN Am 4401, Grand Passage, New Caledonia. Scales represent 0.2 mm.

long as antenna 2; peduncular article 1 short, about as long as broad, with long posterodistal tooth; accessory flagellum 8-articulate, article 1 slightly elongate; callynophore, well-developed 2-field in male and female, with posterodistal setae; flagellum long, 28-articulate (female 23); calceoli present in male and female. *Antenna 2:* about 0.7 times as long as body in male, 0.4 times as long as body in female; peduncle with brush setae in male and female, peduncular articles 4 and 5 not swollen in male or female; calceoli present in male and female.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded. *Mandible:* incisors symmetrical with slightly convex margins; left lacinia mobilis absent; accessory spine row, left and right each with 4 spines; molar setose, strongly spinose; mandibular palp attached midway; article 1 about as long as broad; article 2 elongate, strongly broadened distally, with 10 setae along distal third of medial margin, 5 setae on distolateral corner; article 3 slender, falcate, with 9 proximal D-setae and 4 short E-setae. *Maxilla 1:* inner plate small, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, with 0-1 cusp, ST4 to ST6 large, slender, multicuspidate, ST7 large, multicuspidate medially, STA 2-cuspidate, STB to STD 3- to 4-cuspidate; palp large, 2-articulate, with 4 terminal spines and 1 flag seta. *Maxilla 2:* inner plate three quarters as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 2 (female, left 2, right 3) well-developed nodular spines, oblique setal row reduced with 4-6 plumose setae; outer plate medium size, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, 4 vestigial submarginal setae present; palp well developed, article 2 broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium long, 2.4 times as long as broad; carpus long, 2.5 times as long as broad, 1.1 times as long as propodus; propodus long, subrectangular, 2.6 times as long as broad, tapering distally, posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of 28 medial spines and a row of 7 cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal in size to coxa 3; carpus long, 2.6 times as long as broad, posterior margin broadly lobate; propodus subrectangular, short, 1.4 times as long as broad; palm slightly acute, with straight, minutely serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe, anterior and posterior margins subparallel; male merus/carpus with dense plumose setae, female merus/carpus with sparse simple setae. *Peraeopod 5:* coxa bilobate, anterior lobe slightly produced ventrally; basis expanded with posterior margin deeply serrate. *Peraeopod 7:* basis, posterior margin slightly rounded with sharply rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with small notch on posteroventral corner. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: with few long fine setae; rami subequal in length, inner ramus with moderate constriction. *Uropod 3:* peduncle short, 1.5 times as long as broad, without lateral flange; rami lanceolate, subequal in length; with long fine setae and minutely serrate margins, plumose setae absent in male and female; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (76%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. *Ichnopus malpatun* is a member of the *I. spinicornis* species group. Within this group it forms a subgroup with two other species, *I. wardi* and *I. woodmasoni*, all of which have a deeply serrate posterior margin on the basis of peraeopod 5, a character otherwise found wholly among the *I. taurus* species group. *Ichnopus wardi* and *I. woodmasoni* are easily distinguished from *I. malpatun* by their acutely produced upper lips. There are other minor differences: in *I. malpatun* the palm of gnathopod 2 is not as oblique and not enlarged as in *I. woodmasoni*; the corners of the basis of peraeopods 6 and 7 are more sharply rounded; and the inner ramus of uropod 2 is more slender and not as deeply constricted.

Etymology. 'Malpatun' is from the language of the Riwo people who live on the shores of the Madang Lagoon. It means 'outside the reef', and refers to the habitat of this species.

Distribution. *Ichnopus malpatun* is known only from the northern coast of New Guinea and the Grand Passage, northern New Caledonia, in 95 to 165 m depth.

Ichnopus parriwi n.sp.

Figs 17-18

Type material. HOLOTYPE, female, 11.5 mm, AM P39655, 95 PARATYPES, AM P39656, between Parriwi Point and Rosherville Beach, Middle Harbour, Port Jackson, New South Wales, Australia, 33°48.6'S 151°14.8'E, baited trap at night on mud bottom, 20 m, S. Keable, D. Townsend & J.K. Lowry on the *Flying Scud*, 3-4 July 1988, site 14; 17 PARATYPES, AM P39657, Parriwi Point, Middle Harbour, Port Jackson, New South Wales, Australia, 33°48.5'S 151°14.8'E, baited trap at night on muddy sand bottom, 8 m, S. Keable & J.K. Lowry on the *Flying Scud*, 23-24 Sept. 1988, site 49; 9 PARATYPES, AM P39658, off Clontarf, Middle Harbour, Port Jackson, New South Wales, Australia, 33°48.5'S 151°14.9'E, baited trap at night, 12 m, S. Keable, J.K. Lowry & D. Townsend on the *Flying Scud*, 16-17 July 1988, site 41.

Additional material examined. One male, AM P39659, Watsons Bay, Port Jackson, New South Wales, Australia, 33°51'S 151°16'E, K. Sheard, 11 Feb. 1938.

Diagnosis. Antenna 1: peduncular article 1 with long posterodistal tooth; callynophore with posterodistal spines. Antennae 1 and 2: calceoli in female and male. Upper lip rounded. Mandible: left lacinia mobilis absent; accessory spine row, left with 3, right with 4 spines; molar setose, moderately spinose; palp article 2 slightly broadened distally. Maxilla 1 with ST7 multicuspidate distomedially; palp inner margin distally serrate. Maxilliped: inner plate with 3 nodular spines; palp article 2 very broad. Gnathopod 1: ischium and carpus very long; dactylus with long cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin deeply serrate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with moderate constriction.

Description. Based on holotype female, 11.5 mm and paratype male, 10.5 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, broadly rounded; rostrum absent; eyes reniform, very slightly enlarged in reproductive male. *Antenna 1:* medium length, about 0.3 times as long as body, 0.6 times as long as antenna 2; peduncular article 1 short, as long as deep, with long posterodistal tooth; accessory flagellum 9-articulate (male 7); callynophore, well-developed 2-field in female and male with 6 posterodistal spines; flagellum long, 25-articulate (male 36); calceoli present in female and male. *Antenna 2:*

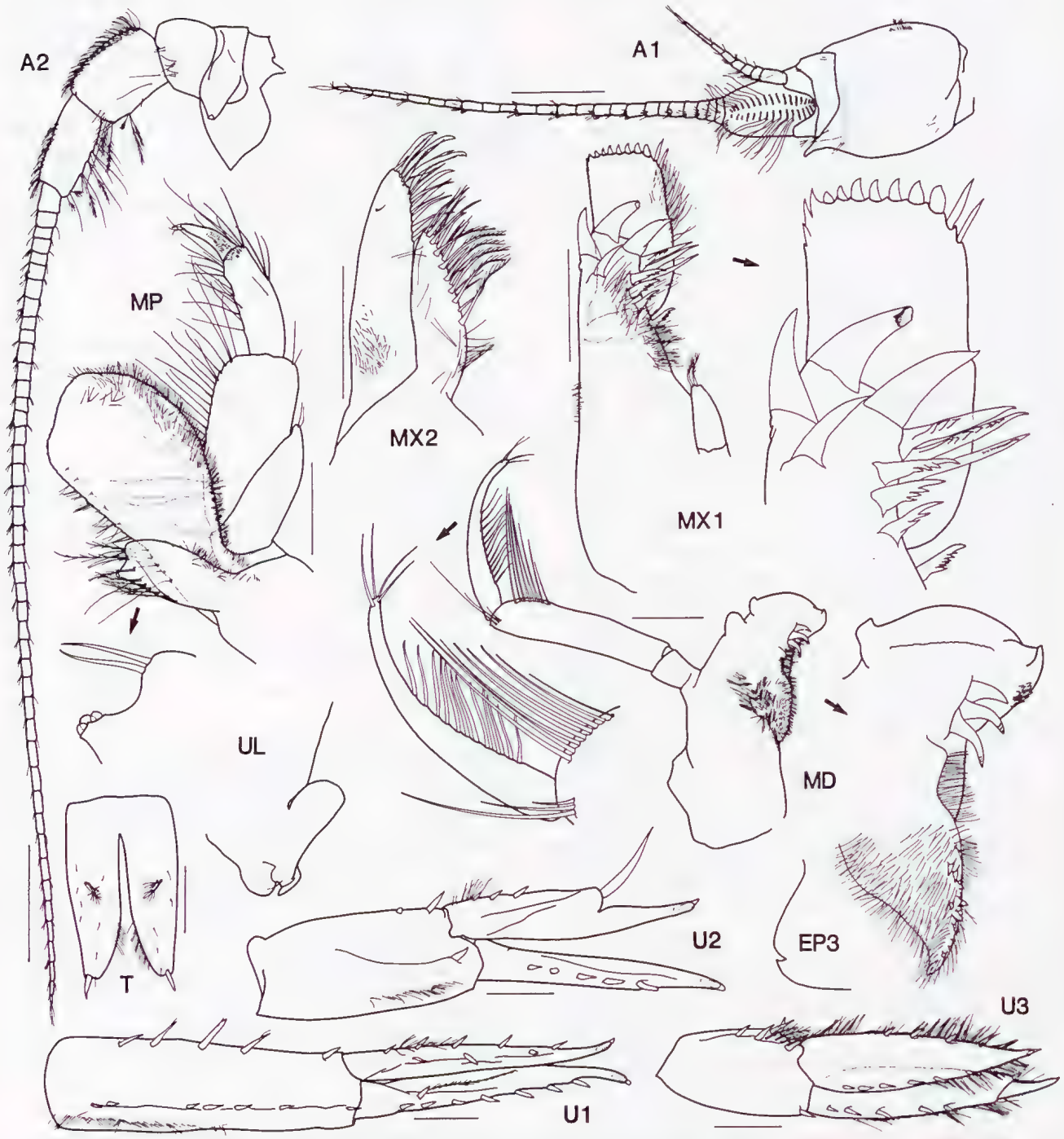

Fig.17. *Ichnopus parriwi* n.sp., holotype female, 11.5 mm, AM P39655, Port Jackson, New South Wales, Australia. Scales for A1,2 represent 0.5 mm, remainder represent 0.2 mm.

about 0.4 times as long as body in female; flagellum 44-articulate and about 0.5 times as long as body in male (52-articulate); peduncle with brush setae in female and male, peduncular articles 4 and 5 not swollen in female or male; calceoli present in female and male.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded. *Mandible:* incisors symmetrical with slightly convex margins; left lacinia mobilis absent, accessory spine row, left with 3 spines, right with 4 spines; molar setose, moderately spinose; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, slightly broadened distally, with 8 setae along distal third of medial margin (male slightly expanded distally, with 6 setae), 3 setae on distolateral corner; article 3 slender, falcate, with 12 (male 9) proximal D-setae and 4 short E-setae. *Maxilla 1:* inner plate small, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, without cusps, ST4 to ST6 large, slender, multicuspidate, ST7 short, multicuspidate distomedially, STA without cusps, STB to STD 3-cuspidate; palp large, 2-articulate, with 7 terminal spines and 2 flag setae. *Maxilla 2:* inner plate three quarters as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 3 well-developed nodular spines, oblique setal row reduced, with 7 plumose setae; outer plate medium size, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, submarginal setae vestigial; palp well developed, article 2 very broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium very long, about 4.9 times as long as broad; carpus very long, 4.7 times as long as broad, 1.4 times as long as propodus; propodus long, subrectangular, 4 times as long as broad, margins subparallel; posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of 23 medial spines and a row of 10 long cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal

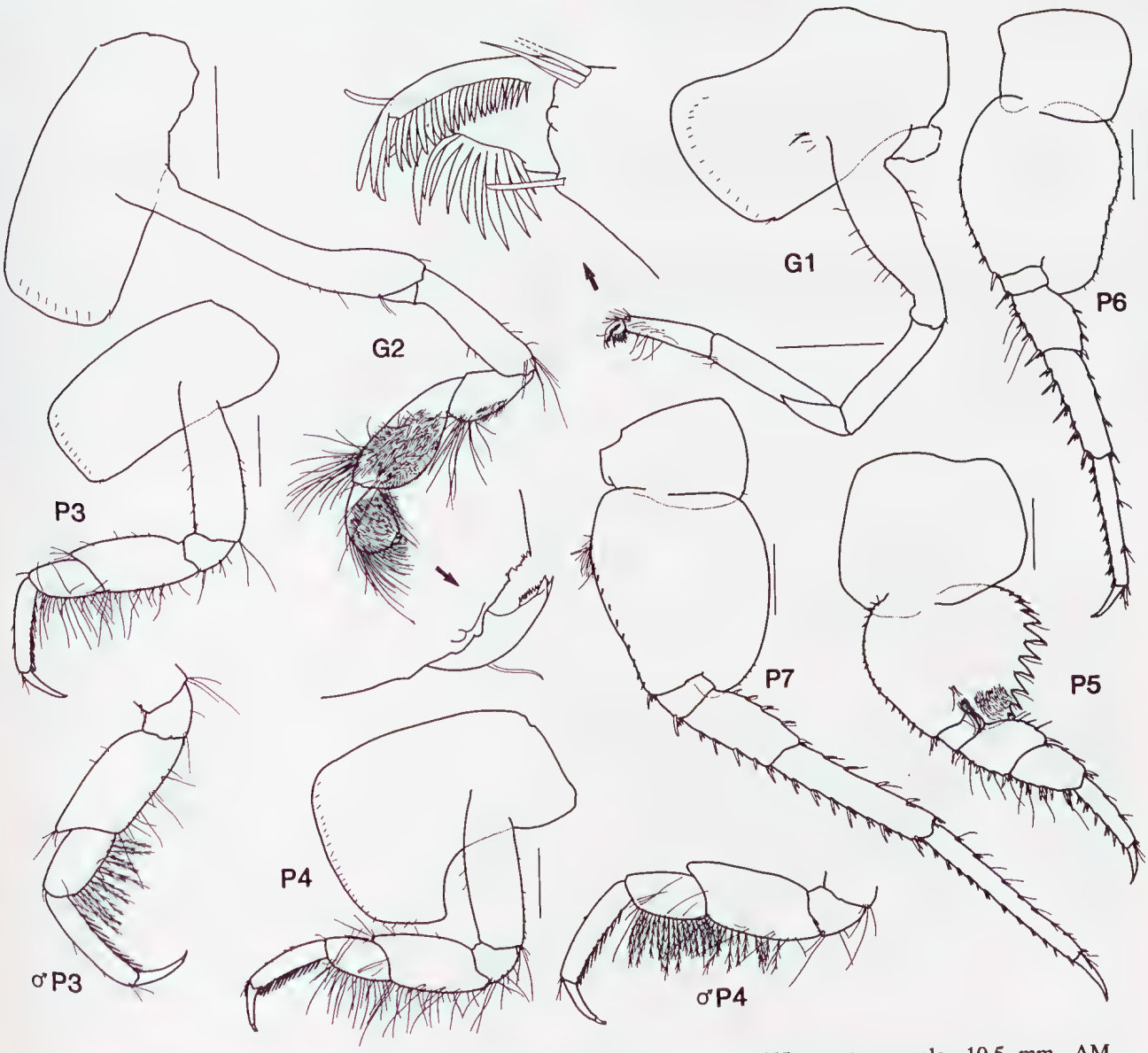

Fig.18. *Ichnopus parriwi* n.sp., holotype female, 11.5 mm, AM P39655, paratype male, 10.5 mm, AM P39656, Port Jackson, New South Wales, Australia. Scales represent 0.5 mm.

in size to coxa 3; carpus long, 2.5 times as long as broad, posterior margin broadly lobate; propodus subrectangular, short, 1.5 times as long as broad; palm slightly acute, with straight, serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe, male merus/carpus with plumose setae. *Peraeopod 5:* coxa bilobate, anterior lobe slightly produced ventrally; basis expanded with posterior margin deeply serrate. *Peraeopod 7:* basis, posterior margin slightly rounded with rounded posteroventral corner and rounded posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with small notch on posteroventral corner. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: with long fine setae; rami subequal in length, inner ramus with moderate constriction. *Uropod 3:* peduncle short, 1.75 times as long as broad, without lateral flange; rami lanceolate, subequal in length with long fine setae and minutely serrate margins; plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (81%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. *Ichnopus parriwi* is a member of the *I. taurus* species group. It is most closely related to *I. tenuicornis* and *I. cribensis* among the species with posterodistal spines on the callynophore. It differs from all species in that group in having calceoli in both males and females.

Ichnopus parriwi appears to be a nocturnal scavenger on muddy bottoms. It has only been found in a small muddy basin surrounded by the sand bottom of Middle Harbour, Port Jackson.

Etymology. Named after Parriwi Point, Middle Harbour, which is very near the type locality.

Distribution. *Ichnopus parriwi* is known only from Port Jackson, Australia in about 20 m depth.

Ichnopus pelagicus Schellenberg

Figs 19-21

Ichnopus pelagicus Schellenberg, 1926: 218.–Schellenberg,1929: 196.–Birstein & Vinogradov, 1964: 163.–J.L. Barnard, 1964: 11, fig.6.–Repelin, 1978: 25, 31, 65, 70, 112, 129, 261, fig.130, tables 1, 2, 5, 7, 13, 17, 49, 61.

? *Socarnes longicornis* Birstein & Vinogradov, 1960: 185, fig.7.–Gurjanova, 1962: 433.

? *Ichnopus nossibeensis* Ledoyer, 1986: 761, figs 294, 295.

Type material examined. LECTOTYPE, male, 10.5 mm, ZMB 20652a, eastern Pacific Ocean, 7°47.5'S 94°05.5'W, 0-550 m, 0800 hours, 31 Dec. 1904, USS *Albatross*, stn 4711; PARALECTOTYPE male, 11 mm, ZMB 22040, *Albatross* stn 4711 (see notes below); PARALECTOTYPE, female, 11 mm, ZMB 22039, eastern Pacific Ocean, 19°00.4'S 125°05.4'W, 0-550 m, 0800 hours, 23 Jan. 1905, USS *Albatross* stn 4736; 3 PARALECTOTYPES, juveniles, 5-8 mm, ZMB 20652b, Indian Ocean, 10°08'S 97°15'W, 0-2400 m, 18 Jan. 1899, German Deep-Sea Expedition, *Valdivia* stn 182.

Schellenberg (1926) originally described this species in the reports of the German Deep-Sea Expedition on the *Valdivia*. He did not specify any type material but recorded three juveniles from *Valdivia* stn 182 and mentioned that the species also occurred in the *Albatross* collections from the eastern Pacific Ocean (listed in Schellenberg, 1929). We borrowed material of *Ichnopus pelagicus* from the Zoological Museum, Berlin. The three *Valdivia* juveniles, ZMB 20652b, (of which one is a male) have at some time dried out and are not in good condition. They had not been dissected. In a separate vial in the same jar was one extensively dissected specimen labelled "4711 male". It seems that this male is the specimen on which Schellenberg based his description

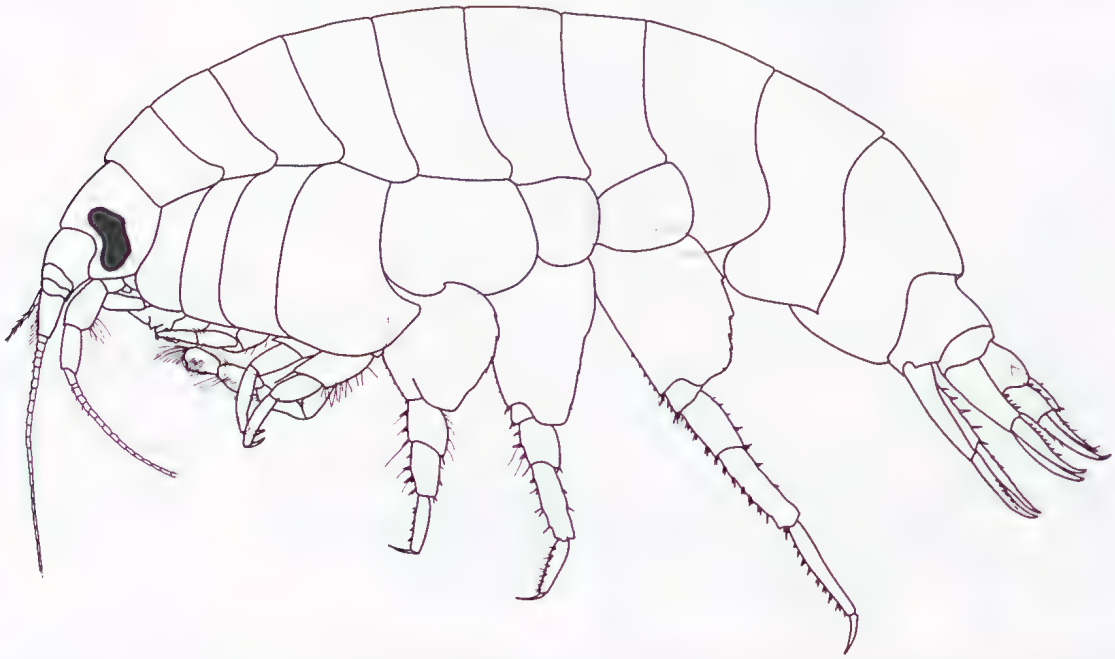

Fig.19. *Ichnopus pelagicus* Schellenberg, female, 10.5 mm, AM P39617, eastern Indian Ocean.

of the species. We have designated it as the lectotype. The mouthparts had been removed but are not in the vial, nor were there any microscope slides. We base our redescription of the species on two other *Albatross* specimens. The juvenile male from *Valdivia* stn 182 has also been dissected and closely compared with the *Albatross* specimens.

Additional material examined. One female, with setose oostegites, 10.5 mm, AM P39617, eastern Indian Ocean, 23°S 110°E, vertical plankton haul, 0-200 m, CSIRO staff on HMAS *Diamantina*, Aug. 1963, Cruise Dm 3/63, stn 118, sample S.1846E; 2 females and 1 immature male, AM P39618, as above except 14°S 110°E, 17 July 1963, stn 102, sample S.1761E, 0755 hours; 1 female, AM P39619, as above except 15°30'S 110°E, 5 Aug. 1963, stn 113, sample S.1815E, 0730 hours; 1 female, AM P39620, as above except 18°30'S 110°E, 6 Aug. 1963, stn 115, sample S.1827E, 0730 hours; 1 specimen, AM P39900, east of Cape York Peninsula, Coral Sea, 10°35.83'S 144°30.65'E, epibenthic sled, 1108-1161 m, P. Hutchings and party on RV *Franklin*, 21 Aug. 1988, stn FR 06/88, stn 6; 2 females and 3 males, AM P40476, 2 females and 2 males, MNHN Paris, Coral Sea, 18°S 164°20'E, R. Repelin, 8 Nov. 1970, Diaphus I, LN 2; 9 specimens (1 ovigerous female) AM P41010, north-east side of Maria Island, Austral Isles, 21°48.2'S 154°44.2'W, plankton tow, 60 m, J.M. Poupin & J.K. Lowry on RV *Marara*, 8 Aug. 1991, FRP-5; 1 ovigerous female, AM P41011, off Rurutu, Austral Isles, 22°29'S 151°21'W, plankton tow, 0-50 m, J.M. Poupin & J.K. Lowry on RV *Marara*, 11 Aug. 1991, FRP-20; 1 male, AM P41012, off Tubuai, Austral Isles, 23°19.5'S 149°31.0'W, plankton sample, estimated depth 50-100 m, J.M. Poupin & J.K. Lowry on RV *Marara*, 13 Aug. 1991, FRP-37.

Diagnosis. Antenna 1: peduncular article 1 with short posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli present in female and male. Upper lip rounded. Mandible: left lacinia mobilis absent; accessory spine row, left and right each with 4 spines; molar setose, strongly spinose; palp article 2 strongly broadened distally. Maxilla 1 with ST7 multicuspidate medially; palp inner margin distally serrate. Maxilliped: inner plate with 2 nodular spines; palp article 2 very broad. Gnathopod 1: ischium and carpus long; dactylus with short cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin minutely crenate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus without constriction.

Description. Based on paralectotype female, 11 mm and paralectotype male, 11 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, narrowly rounded; rostrum absent; eyes reniform, slightly enlarged in reproductive male. *Antenna 1:* medium length, about 0.3 times as long as body; peduncular article 1 short, about as long as broad, with posterodistal tooth; accessory flagellum broken (male 7-articulate, article 1 elongate); callynophore, well-developed 2-field

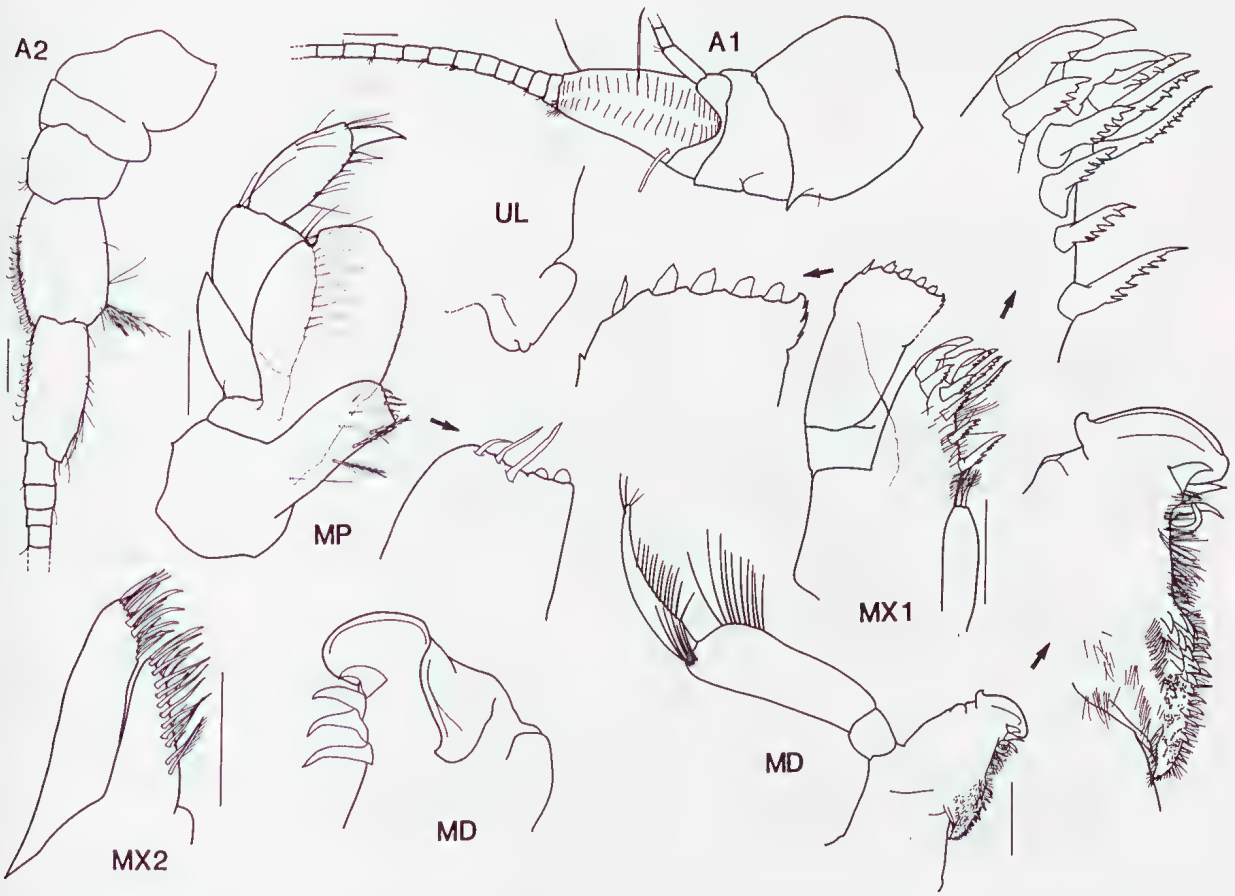

Fig.20. *Ichnopus pelagicus* Schellenberg, paralectotype female, 11 mm, ZMB 22039, eastern Pacific Ocean. Scales represent 0.2 mm.

in female and male with posterodistal setae; flagellum broken at article 15, (long, 34-articulate in male), calceoli present in male (flagellum articles 6, 9, 10, 12-18) and female (a calceolus on article 6). *Antenna 2:* half as long as body in female; flagellum 52-articulate, at least 0.6 times as long as body in male (at least 44-articulate); peduncle with brush setae in female and male, peduncular articles 4 and 5 not swollen in female or male; calceoli present in male on flagellum articles 1-3, 5-7, 11, 15, 19, 21, 27, 29, 31, 32, 34, 37, 39.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded. *Mandible:* incisors symmetrical with slightly convex margins; left lacinia mobilis absent; accessory spine row, left and right each with 4 spines; molar setose, strongly spinose; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, strongly broadened distally, with 10 (male 12) setae along distal third of medial margin, 6 (male 7) setae on distolateral corner; article 3 strongly falcate with 4 short E-setae, 12 (male 12) proximal D-setae, B-setae absent. *Maxilla 1:* inner plate small, narrow with 2 apical plumose setae; outer

Fig.21. *Ichnopus pelagicus* Schellenberg, paralectotype female, 11 mm, ZMB 22039, paralectotype male, 11 mm, ZMB 22040, eastern Pacific Ocean. Scales for U1-3, T represent 0.2 mm, remainder represent 0.5 mm.

plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, weakly cuspidate, ST4 to ST6 large, slender, multicuspidate, ST7 long, multicuspidate medially, STA 2- to 3-cuspidate, STB to STD 5-cuspidate; palp large, 2-articulate, with 4 terminal spines and 1 flag seta. *Maxilla 2:* inner plate about three quarters times as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 2 well-developed nodular spines, oblique setal row weakly developed, with 3 plumose setae; outer plate medium size, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, 3 vestigial submarginal setae present; palp well developed, article 2 very broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium long, twice as long as broad; carpus long, twice as long as broad, as long as propodus; propodus long, 2.3 times as long as broad, tapering distally; posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of about 15 small medial spines and a row of 5 small cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal in size to coxa 3; carpus long, 2.6 times as long as broad, posterior margin broadly lobate; propodus subrectangular, short, 1.3 times as long as broad; palm slightly acute, with concave, minutely serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe, male and female merus/carpus with plumose setae. *Peraeopod 5:* coxa equilobate; basis expanded with posterior margin minutely crenate. *Peraeopod 7:* basis, posterior margin slightly rounded with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: posteroventral corner with a tiny notch. *Uropod 1*: with few long fine setae; rami subequal in length. *Uropod 2*: without long fine setae; rami subequal in length, inner ramus without constriction. *Uropod 3:* peduncle short, 1.3 times as long as broad without lateral flange; rami lanceolate, subequal in length, with long fine setae and minutely serrate margins, plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (75%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. There is not enough material of *Ichnopus pelagicus* available for study to be certain about its species limits. We have seen specimens from the eastern and western South Pacific Ocean, the Coral Sea and the eastern and western Indian Ocean and although there are slight differences in populations from different areas they do not appear to us to be separate species. Calceoli are scarce on the female antennae and occasionally absent. The posteroventral notch on epimeron 3 is weak, but always present. Consequently we have left *I. longicornis* Birstein & Vinogradov in synonymy and also included *I. nossibeensis* Ledoyer. Ledoyer (1986) thought that the weak cuticular spines on the posterior margin of the dactylus in gnathopod 1 would distinguish the south-western Indian Ocean population from *I. pelagicus*, but our figures of *I. pelagicus* from the eastern Pacific and from the eastern Indian Ocean are extremely similar to those of *I. nossibeensis*. However, the mouthparts of *I. longicornis* and *I. nossibeensis* are not well known. Until these characters are fully studied we cannot be certain.

Within the *I. spinicornis* species group *I. pelagicus* is most closely related to *I. annasona*, but they are easily distinguished because *I. annasona* has a strongly constricted inner ramus on uropod 2.

Repelin (1978) commented on the ecology of *I. pelagicus* as part of his monograph on the pelagic amphipods of the western and central Pacific Ocean. He found that: *I. pelagicus* was a tropical epipelagic species taken most frequently at night; although it was not common compared with hyperiidean amphipods it was the most frequently occurring lysianassoid amphipod; and it was an occasional food item of the hatchet fish *Sternoptyx diaphana* Hermann.

Distribution. *Ichnopus pelagicus* is known from pelagic waters in the eastern and western South Pacific Ocean and from the eastern and western Indian Ocean. Repelin (1978) did not find it in his collections from the central Pacific. Farthest north collections are those of Birstein & Vinogradov (1960) from 19°N, east of Mariana Islands in the western Pacific, and farthest south is 23°S in both the Indian and Pacific Oceans, in upper 200 m of water.

Ichnopus pseudoserricrus Ledoyer

Fig. 22

Ichnopus pseudoserricrus Ledoyer, 1986: 763, fig.296.

Material examined. 3 specimens, largest 6.5 mm, sex not determinable, MNHN Am 2223, Nosy Bé, Madagascar, western Indian Ocean [approx. 13°22'S 48°16'E], plankton tow, stn NBH 14.

Diagnosis. Antenna 1: peduncular article 1 with long posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli present. Upper lip rounded. Mandible: left lacinia mobilis present; accessory spine row, left and right each with 4 spines; molar setose, strongly spinose; palp article 2 strongly broadened distally. Maxilla 1 with ST7 multicuspidate medially; palp inner margin distally serrate. Maxilliped: inner plate with 3 nodular spines; palp article 2 broad. Gnathopod 1: ischium and carpus long; dactylus with short cuticular spines. Gnathopod 2: palm not known for female. Peraeopod 5: basis with posterior margin strongly crenate. Epimeron 3: posteroventral corner

with small notch. Uropod 2: inner ramus with moderate constriction.

Remarks. Ledoyer (1986) was misled by Walker's (1909) poor description of *I. serricrus*, particularly his description of the telson. Nonetheless, the 6.5 mm specimen of *I. pseudoserricrus* which we have examined differs from *I. serricrus* in having 4 accessory spines on the left mandible, maxilla 1 outer plate with ST7 large, multicuspidate medially, STA 1-cuspidate, STB to STD 2-cuspidate. It also has calceoli on antennae 1 and 2, a 2-field callynophore with posterodistal setae and a produced, rounded upper lip.

Ichnopus pseudoserricrus is a member of the *I. spinicornis* species group. *Ichnopus pseudoserricrus* and *I. serricrus* appear to be sister taxa, one with an extensive distribution and the other with a limited distribution. Both species are easily distinguished from other species in the group because they have a strongly crenate posterior margin on the basis of peraeopod 5.

Distribution. *Ichnopus pseudoserricrus* is known only from surface plankton off Nosy Bé, Madagascar.

Ichnopus serricrus Walker

Figs 23-24

Ichnopus serricrus Walker, 1909: 328, pl.43 fig.1.–Thurston & Allen, 1969: 359.–Echelman & Fishelson, 1990a: 182 (table 2), 185.–Echelman & Fishelson, 1990b: 70 (table 1).

Ichnopus taurus.–Spandl, 1924: 43, fig.15.

Type material. LECTOTYPE, male, 10 mm, BMNH 1909.1.29:14-16 and 1909.2.13:3 (slide), Amirante Islands, Indian Ocean [approx. 6°00'S 53°10'E], dredged, 40-155 m, J.S. Gardiner on HMS *Sealark*, 11 Oct. 1905, stn E10; PARALECTOTYPE, female, 8 mm, BMNH 1909.1.29:14-16, Coco Island, Cargados Islands, Indian Ocean [approx. 16°35'S 59°40'E] plankton tow at surface, J.S. Gardiner on HMS *Sealark*, 30 Aug. 1905, stn (i).

Walker (1909) recorded his material as two males. We have examined his syntype material and found that the specimen from Coco Island is a female with non-setose oostegites. The male from Amirante Islands, here designated as lectotype, is the specimen Walker partially dissected and illustrated. There are some discrepancies between Walker's account of the species and our observations. Antenna 2 of the male does have calceoli. The telson does have distal spines, set in a slight notch, although the left lobe of the male is damaged. Both third uropods are missing from both specimens and none are mounted on the slide. This makes Walker's account of the urosome somewhat dubious. It appears that his description of uropod 3 is based on a misinterpretation of uropod 2: the "2nd joint" is really the distal section of the inner ramus of uropod 2, beyond the deep constriction; the "curved spine" is obvious in uropod 2.

Additional material examined. 114 specimens from 17 collections, off Elat, Gulf of Aqaba, Red Sea, [approx. 29°30'N 34°57'E], plankton tows, collected by L. Fishelson, as follows: 2 males, 1 female, 1 juvenile, AM P39626, surface tow, 13 Oct. 1985, stn RS 85-02; 2 males, 16 juveniles, AM P39627, surface tow, 13 Oct. 1985, stns RS 85-14, 15, 16; 3 males, AM P39628, surface tow, 12 Dec. 1985, stn RS 85-114; 2 males, BMNH 1990:34:2, surface tow, 12 December 1985, stn RS 85-128; 5 males, L. Fishelson collection, surface tow offshore, 12 Dec. 1985, stn RS 85-134; 38 males, 2 immature females, 14 juveniles, AM P39629, surface tow at night, 5 Dec. 1985, stns RS 85-145, 149; 1 male, AM P39630, vertical haul, 0-100 m, night, 21 Nov. 1985, stn RS 85-174;

Fig.22. *Ichnopus pseudoserricrus* Ledoyer, unknown sex, 6.5 mm, MNHN Am 2223, Madagascar, western Indian Ocean. Scales represent 0.1 mm.

1 ?female, 10 juveniles, AM P39631, surface tow at night, 21 Nov. 1985, stns RS 85-182, 183, 184; 1 immature male, AM P39632, vertical haul, 0-100 m, night, 12 Dec. 1985, stn RS 85-189; 10 males, AM P39633, surface tow at night, 12 Feb. 1986, stn RS 86-204; 2 males, USNM 253720, surface tow at night, 12 Feb. 1986, stn RS 86-205; 3 juveniles, AM P39634, surface tow at night, 12 Dec. 1985, stn RS 85-176.

Fig.23. *Ichnopus serricrus* Walker, lectotype male, 10 mm, BMNH 1909.1.29:14-16, Amirante Islands, Indian Ocean; whole animal: male, 9 mm, AM P39626, Gulf of Aqaba, Red Sea. Scales represent 0.1 mm.

22 specimens from 9 collections, off Elat, Gulf of Aqaba, Red Sea, [approx. 29°30'N 34°57'E], surface plankton tows, collected by T. Echelman, as follows: 12 specimens, AM P39635, 1500 m offshore, 1500 hours, 21 Nov. 1985, stn TE-12; 2 specimens, AM P39636, 100 m offshore, 1805 hours, 12 Dec. 1985, stn TE-28; 4 specimens, AM P39637, 2000 m offshore, 1905 hours, 13 Feb. 1986, stn TE-67; 1 specimen, AM P39638, 100 m offshore, 2030 hours, 29 May 1986, stn TE-90; 2 specimens, AM P39639, 2000 m offshore, 1945 hours, 1 Dec. 1986, stn TE-131; 2 specimens, AM P39640, 2000 m offshore, 1951 hours, 17 Dec. 1986, stn TE-148; 1 specimen, AM P39641, 2000 m offshore, 1930 hours, 3 Jan. 1987, TE-160; 1 specimen, AM P39642, 40 m offshore, 2007 hours, 17 Feb. 1987, TE-204; 2 specimens, 1000 m offshore, 2143 hours, 24 Mar. 1987, stn TE-216.

6 specimens, NMW, from 5 plankton collections, *Pola*-Expedition to Red Sea, 1896-1898, as follows: 1 male, stn 77, 27°34'N 34°56'E; 1 specimen, stn 82, 26°44'N 35°09'E; 2 females, stn 89, 28°40'N 32°57'E; 1 female, stn 100, 26°57'N 34°12'E; 1 specimen, stn 158, 24°58'N 35°46.7'E.

1 ?female, MNHN Paris, off La Réunion, Indian Ocean, 21°5.6'S 55°13.3'E, Charcot-Picard dredge, 80-83 m, black sand, 22 Aug. 1982, MS *Marion-Dufresne*, campagne MD-32, stn DC 54.

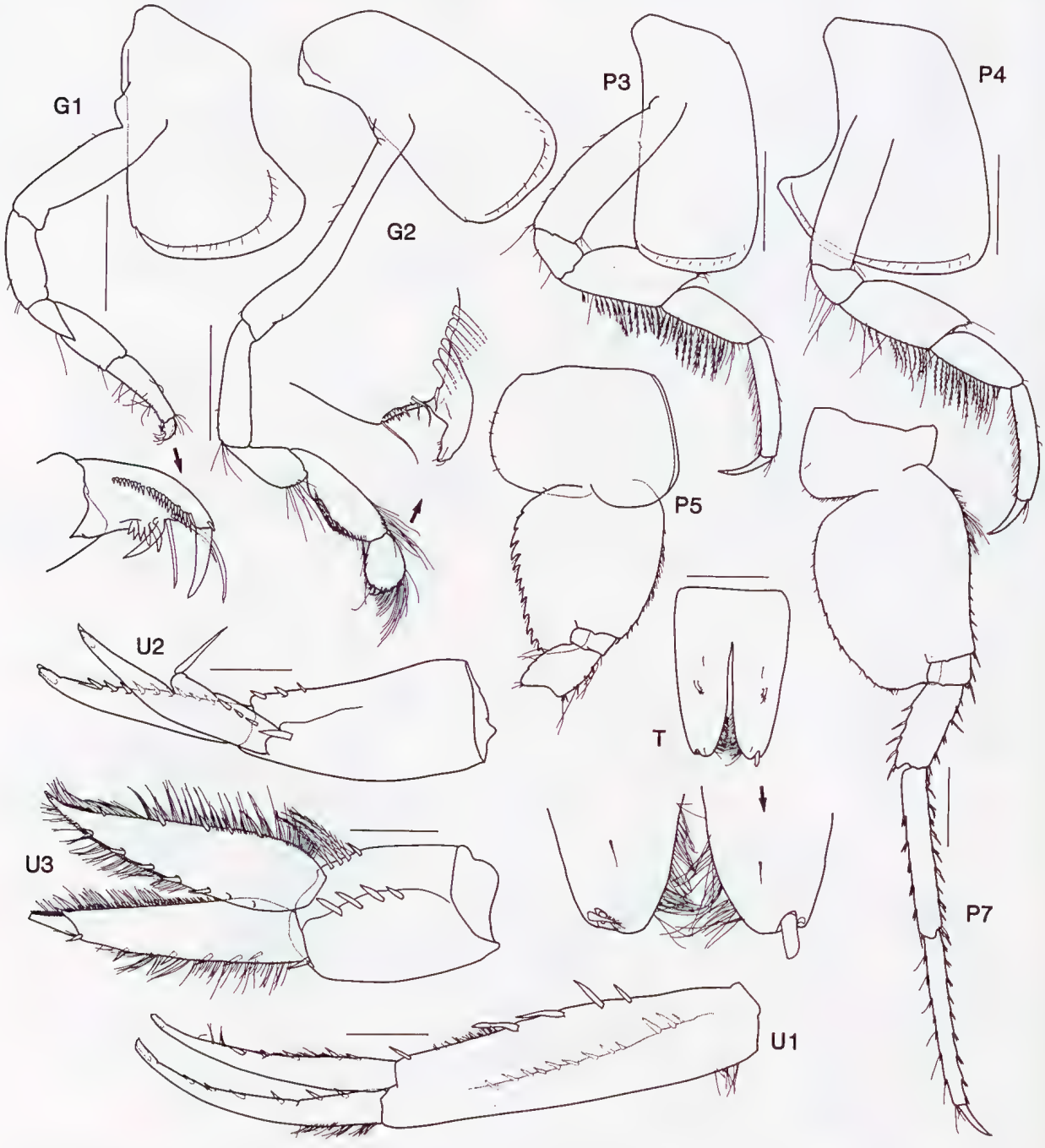

Fig.24. *Ichnopus serricrus* Walker, lectotype male, 10 mm, BMNH 1909.1.29:14-16, Amirante Islands, Indian Ocean; P7, U3: male, 9 mm, AM P39626, Gulf of Aqaba, Red Sea. Scales for U1-3, T represent 0.2 mm, remainder represent 0.5 mm.

Diagnosis. Antenna 1: peduncular article 1 with long posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli present in male only. Upper lip subacute. Mandible: left lacinia mobilis present; accessory spine row, left with 3, right with 4 spines; molar setose, strongly spinose; palp article 2 strongly broadened distally. Maxilla 1 with ST7 multicuspidate distally; palp inner margin distally serrate. Maxilliped: inner plate with 3 nodular spines; palp article 2 broad. Gnathopod 1: ischium and carpus long; dactylus with short cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin strongly crenate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with moderate constriction.

Description. Based on lectotype male, 10 mm and paralectotype female, 8 mm; characters not known from type material based on 7.5 mm female and 9 mm male from the Red Sea, AM P39626. *Head*: slightly deeper than long, lateral cephalic lobe well developed, rounded; rostrum absent; eyes reniform, enlarged in reproductive male. *Antenna 1:* medium length, about 0.36 times as long as body, 0.60 times as long as antenna 2; peduncular article 1 short, about as long as broad, with long posterodistal tooth; accessory flagellum 10-articulate, article 1 not elongate; callynophore, well-developed 2-field in female and male, apparently without posterodistal setae or spines (setae may be present; the callynophore is exceptionally dense and obscures the posterodistal corner; material from La Réunion and the Red Sea has posterodistal setae); flagellum long, at least 27-articulate in male, 31-articulate in female; calceoli present in male (articles 4-20, 22, 24), not present in female. *Antenna 2:* elongate (flagellum 53-articulate in male), 0.6 times as long as body in reproductive male; peduncle with brush setae in male and female, peduncular articles 4 and 5 not swollen in female or male; calceoli present on most articles in male.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, subacute. *Mandible:* incisors symmetrical, with slightly convex margins; left lacinia mobilis present, a tiny spine; accessory spine row, left with 3 spines, right with 4 spines; molar setose, strongly spinose; mandibular palp attached midway, article 1 short, about as long as broad; article 2 elongate, strongly broadened distally, with 13 setae along distal third of medial margin; article 3 slender, falcate, with 11 proximal D-setae and 4 short E-setae. *Maxilla 1:* inner plate small, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, weakly cuspidate, ST4 to ST6 large, slender, multicuspidate, ST7 large, multicuspidate distally, STA to STD 2- to 3-cuspidate; palp large, 2-articulate, with 5 terminal spines and 1 flag seta. *Maxilla 2:* inner plate 0.8 times as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 3 well-developed nodular spines, oblique setal row reduced, with 8 plumose setae; outer plate medium size, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, 4 vestigial submarginal setae present; palp well developed, article 2 broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium long, about 2.5 times as long as broad; carpus long, 2.5 times as long as broad, 1.1 times as long as propodus; propodus long, subrectangular, 3 times as long as broad, tapering distally; posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of 23 medial spines and a row of 6 short cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal in size to coxa 3; carpus long, 2.7 times as long as broad, posterior margin broadly lobate; propodus subquadrate, short, 1.2 times as long as broad; palm acute, with straight, minutely serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe, male and female merus/carpus with plumose setae. *Peraeopod 5:* coxa equilobate; basis expanded with posterior margin strongly crenate. *Peraeopod 7:* basis, posterior margin slightly rounded with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with small notch on posteroventral corner. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: without long fine setae; rami subequal in length, inner ramus with moderate constriction. *Uropod 3:* peduncle short, 1.3 times as long as broad without lateral flange; rami lanceolate, subequal in length, with long setae and minutely serrate margins, plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (70%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. *Ichnopus serricrus* is a member of the *I. spinicornis* species group. Aside from its sibling relationship with *I. pseudoserricrus*, discussed under that species, it shows no strong relationship to any other member of the group. *Ichnopus serricrus* is easily distinguished from other species in the group, except for *I. pseudoserricrus*, by the strongly crenate posterior margin on the basis of peraeopod 5.

Echelman & Fishelson (1990) found that *I. serricrus* was the third most abundant gammaridean amphipod in their study of the community structure of surface plankton near the reef in the Gulf of Aqaba. They found that *I. serricrus* was more abundant 2 km off the reef than it was near the reef indicating that it is a true pelagic species.

Distribution. *Ichnopus serricrus* is an inshore species known in the western Indian Ocean from Madagascar to the Gulf of Aqaba.

Ichnopus spinicornis Boeck

Figs 25-26

Ichnopus spinicornis Boeck, 1861: 645.–Boeck, 1871: 98.–Chevreux, 1888: 39.–Sars, 1890: 40, pl.15.–Sars, 1895: 675.–Norman, 1895: 479.–Chevreux, 1898: 476.–Chevreux, 1900: 15.–Norman, 1900: 142.–Stebbing, 1906: 52, fig.10.–Walker, 1910: 159.–Nordgaard, 1911: 21.–Sexton, 1911: 200.–Tattersall, 1913: 3.–Stephensen, 1915: 35.–Stephensen, 1923: 78.–Chevreux & Fage, 1925: 47, figs 28, 29.–Chevreux, 1927: 56.–Stephensen, 1929a: 61.–Stephensen, 1929b: 2.–Stephensen, 1935: 64.–Cecchini & Parenzan, 1935: 162, fig.6.–Chevreux, 1935: 36.–Stephensen, 1942: 472.–Gurjanova, 1951: 220, fig.86.–Reys, 1960: 90.–Toulmond & Truchot, 1964: 6.–Macquart-Moulin, 1968: 313.–Poizat, 1969: 402.–Vader, 1969: 6.–Bellan-Santini & Ledoyer, 1973: 919.–Krapp-Schickel, 1974: 322, 337.–Ledoyer, 1977: 374.–Drago *et al.*, 1978: 75.–Vader & Johannessen, 1978: 336.–Lincoln, 1979: 94, fig.38.–Mattson, 1981: 115 (table 1).–Macquart-Moulin, 1984: 185.–Marques & Bellan-Santini, 1985: 323, 349.–Tully & Ó Céidigh,

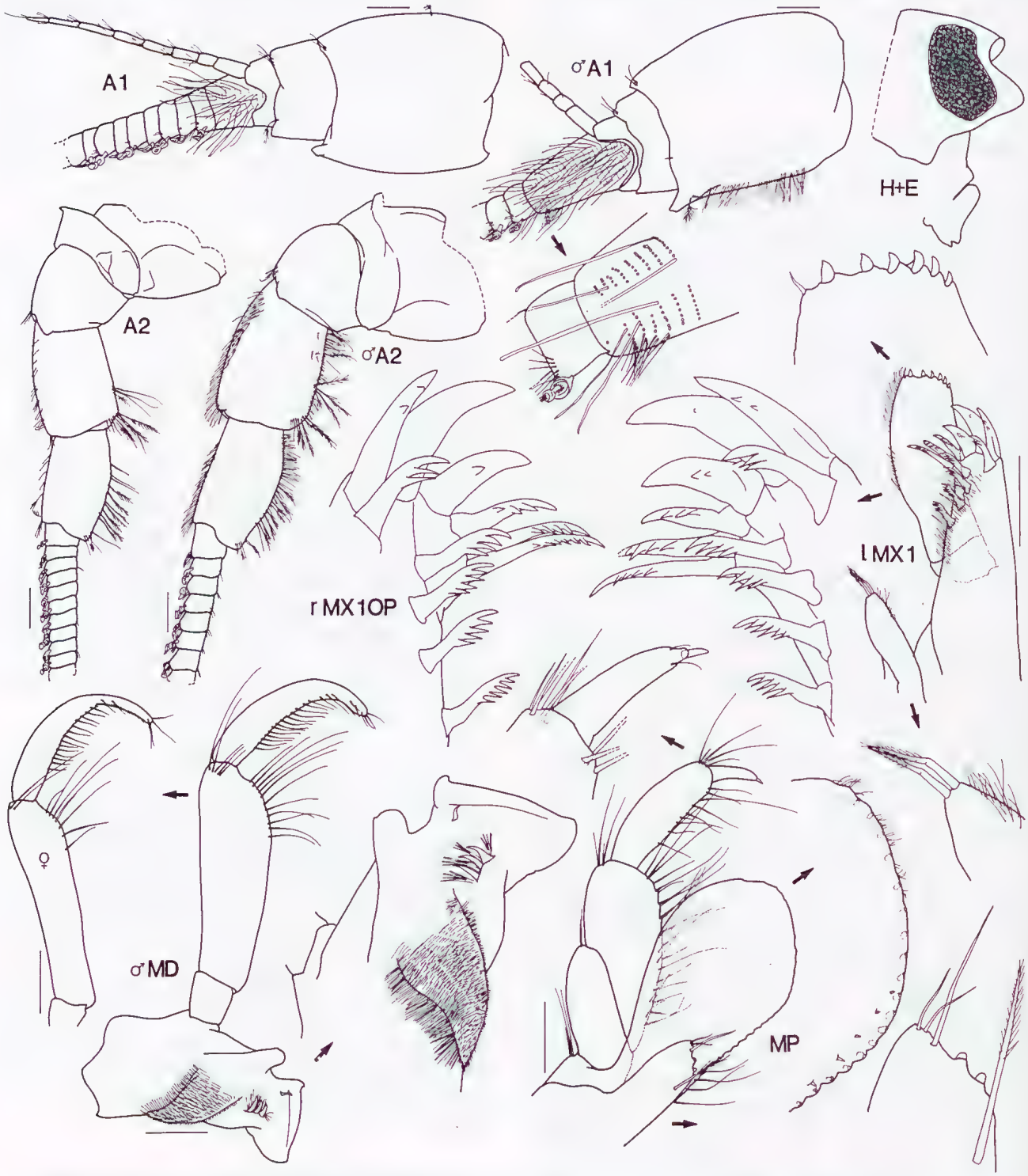

Fig.25. *Ichnopus spinicornis* Boeck, female, 14.5 mm, male, 15.5 mm, AM P40072, Masfjorden, Norway. Scales represent 0.2 mm.

1987: 62.–Dauvin & Toulemont, 1988: 218 (table 1).–Costello *et al.*, 1989: 33.–Diviacco & Ruffo, 1989: 486, fig.329.–Kaartvedt, 1989: 189.–Palerud & Vader, 1991: 36.
Lysianassa spinicornis.–Lilljeborg, 1865a: 20.–Lilljeborg, 1865b: 11.
Ichnopus calceolatus Heller, 1866: 20, pl.2 figs 26-28.–Marion, 1883: 44.–Krapp-Schickel, 1974: 322, 337.
Ichnopus minutus Boeck, 1871: 99.

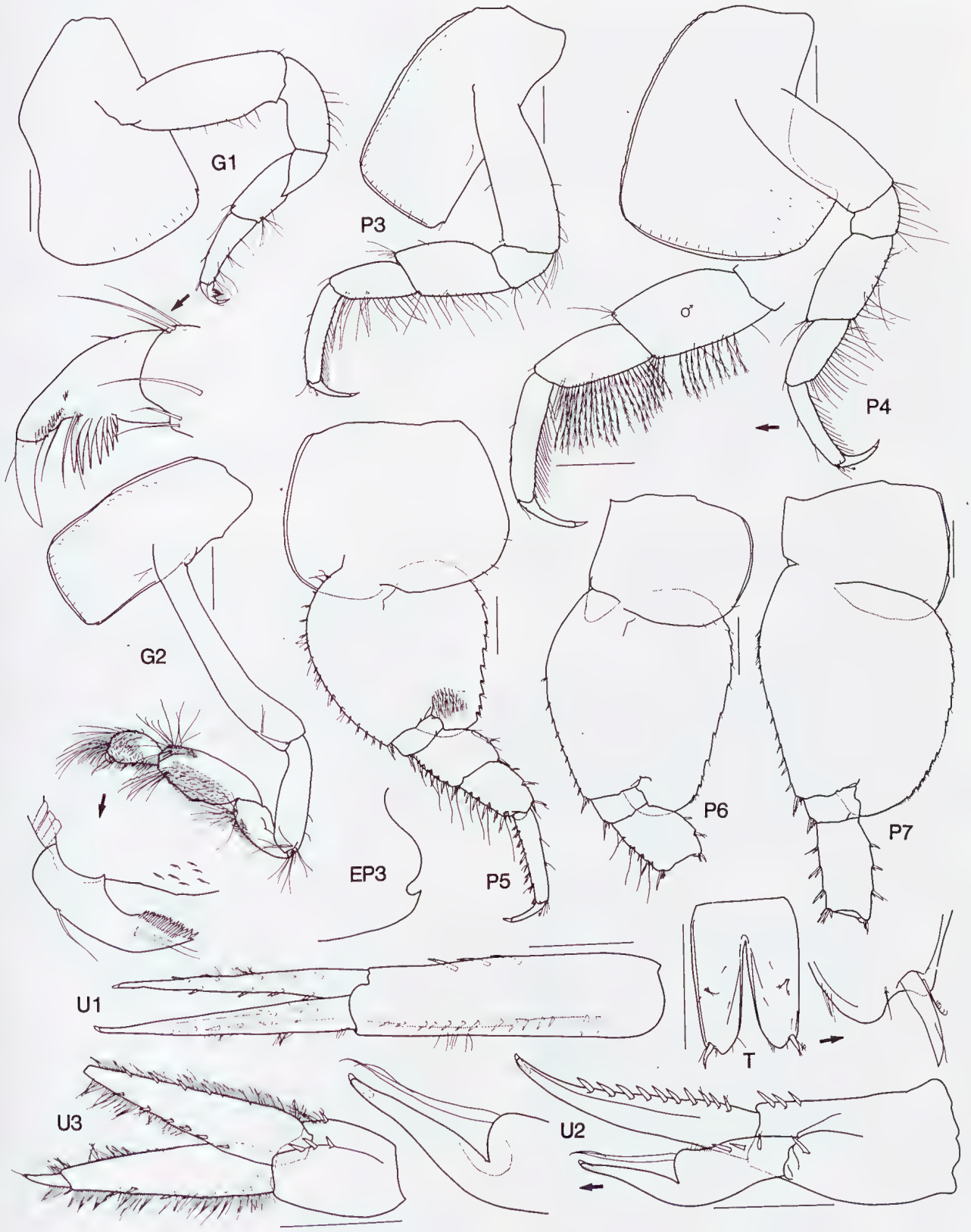

Fig.26. *Ichnopus spinicornis* Boeck, female, 14.5 mm, male, 15.5 mm, AM P40072, Masfjorden, Norway. Scales represent 0.5 mm.

Ichnopus taurus.–Della Valle, 1893: 801, pl.27 figs 1-22 (in part).

not *Ichnopus spinicornis*.–Ledoyer, 1986: 764, fig.297 (= *I. comorensis*).

Material examined. 16 females, 15 males, 10 juveniles, AM P40066 to P40074, P40076, Masfjorden, western Norway, approximately 60°49'N 5°23'E, pumped at night, 36-75 m over bottom depth of 80-85 m, S. Kaartvedt on RV *Håkon Mosby*, Dec. 1986 and Apr. 1987; 1 specimen, ZMUB 9569, Lyrenes, Byford, Norway, coll. Nordgaard; 1 specimen, ZMUB 17486, Bergen, Norway; 1 specimen, ZMUB 19873, Filjar, Norway, 20-40 m, June 1890, coll. Grieg; 1 specimen ZMUB 46456, west of Sandtorg, Norway, 15-35 m, Tambs - Lyche, 29 June 1954, stn M-17/62; 2 specimens, ZMUB 58917, Narøy-Viksø, Korsfjorden, Norway, shelly sand, stone, *Laminaria*, 8.5 m, 14 Apr. 1965, stn B.S. 392-65; 1 specimen ZMUB 58918, Korsfjorden, Norway, 690 m, 11 Apr. 1969, stn E129-69; 1 female, 2 males, 1 juvenile, ZMUB 58919, Liholmstennen, Raunefjord, Norway, 100-130 m, 5 Apr. 1972, stn E51-72; 1 specimen, ZMUB 61196 south-west of Bjellandsøene, Husnesfjord, Norway, 59°49'N 5°41'50"E, 120 m, 29 Nov. 1961, stn Z.14/61.

One ovigerous female, 15.5 mm, AM P40477, Bendo Palummo, Gulf of Naples, Mediterranean Sea, 105 m, U. Schiecke, 23 Dec. 1974; 1 ovigerous female, 9.5 mm, MCSN Verona, Ischia - P.S. Pancrazio, Gulf of Naples, Mediterranean Sea, 40 m, U. Schiecke, 19 Sept. 1969.

Diagnosis. Antenna 1: peduncular article 1 with long posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli present in female and male. Upper lip rounded. Mandible: left lacinia mobilis present; accessory spine row, left with 3, right with 4 spines; molar setose, without spines; palp article 2 slightly broadened distally in female, more strongly in male. Maxilla 1 with ST7 multicuspidate medially; palp inner margin distally smooth. Maxilliped, inner plate with 2 nodular spines; palp article 2 broad. Gnathopod 1: ischium and carpus long; dactylus with short cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin minutely crenate. Epimeron 3: posteroventral corner with large notch. Uropod 2: inner ramus with strong constriction.

Description. Based on female, 14.5 mm and male, 15.5 mm, AM P40072 and fully mature male, 20 mm, ZMUB 58919. *Head*: slightly deeper than long, lateral cephalic lobe well developed, narrowly rounded; rostrum absent; eyes reniform, slightly enlarged in reproductive male. *Antenna 1:* medium, about 0.3 (male 0.5) times as long as body, 0.7-0.8 times as long as antenna 2; peduncular article 1 short, 1.4 times as long as broad, with long posterodistal tooth; accessory flagellum 8-articulate (male 10), article 1 slightly elongate; callynophore, well-developed 2-field in female and male, with posterodistal setae; flagellum long, 65-articulate (male 86); calceoli present in male and female. *Antenna 2:* elongate, as long as body in reproductive male; peduncle with brush setae in male and female, peduncular articles 4 and 5 not swollen in male or female; calceoli present in male and female. *Mouthpart bundle*: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded. *Mandible:* incisors symmetrical, slightly convex margins; left lacinia mobilis a tiny slender spine; accessory spine row, left with 3 and right with 4 spines; molar setose, without spines; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, slightly broadened distally (male more so), with 7 (male 11) setae along distal third of medial margin and 2 (male 5) setae on distolateral corner; article 3 slender, falcate, with about 16 (male 19, extending to tip of article 3) proximal D-setae, and 3 short E-setae. *Maxilla 1:* inner plate small with 2 apical plumose setae; outer plate extremely narrow with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, with 0-1 cusp, ST4 to ST6 large, slender, multicuspidate medially, ST7 large, multicuspidate medially, STA to STD short, 2- to 5-cuspidate; palp large, 2-articulate, with 4 terminal spines and 1 flag seta. *Maxilla 2:* inner plate nearly as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 2 well-developed nodular spines, oblique setal row reduced, with 1 plumose seta; outer plate medium size, subovate, apical setae and spines absent, medial spines present, reduced in size, bead-shaped, vestigial submarginal setae present; palp well developed, article 2 broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium long, 2.3 times as long as broad; carpus long, 2.4 times as long as broad, 1.2 times as long as propodus; propodus long, subrectangular, 3 times as long as broad, tapering distally, posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of 10 medial spines and a row of 8 cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal in size to coxa 3; carpus long, 2.8 times as long as broad, posterior margin broadly lobate; propodus subrectangular, short, 1.8 times as long as broad; palm acute, with straight minutely serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe; male merus/carpus with plumose setae. *Peraeopod 5:* coxa equilobate; basis expanded with posterior margin minutely crenate. *Peraeopod 7:* basis, posterior margin slightly rounded with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with strong notch above posteroventral corner. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: with long fine setae; rami subequal in length, inner ramus with strong constriction. *Uropod 3:* peduncle short, 1.8 times as long as broad, without lateral flange; rami lanceolate, subequal in length, with long fine setae and minutely serrate margins, plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (76%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. *Ichnopus spinicornis* has many

plesiomorphic character states. It differs from other members of the *I. spinicornis* species group in not having spines on the mandibular molar, and does not appear to be closely related to any member of the group except *I. comorensis*. Specimens collected from Masfjorden, Norway show an almost equal sex ratio indicating that *I. spinicornis* is a true pelagic species.

The *I. spinicornis* of Ledoyer (1986), described here as *I. comorensis* n.sp., differs from *I. spinicornis* in having significantly fewer articles in the flagella of antennae 1 and 2, in the shape of the carpus of gnathopod 1 and in the small notch on the posteroventral margin of epimeron 3. The smaller of the two females in our material examined from the Gulf of Naples differs from other material of *I. spinicornis* in eye colour, size of adult female and number of cusps on maxilla 1 STA. It may indicate the presence of more than one *I. spinicornis*-like species in the Mediterranean Sea.

Distribution. *Ichnopus spinicornis* is known from Norway to the Mediterranean Sea in depths from 15 to 690 m.

Ichnopus taurus Costa

Figs 27-28

Ichnopus taurus Costa, 1853: 172.–Costa, 1857: 189, pl.1 fig.3.–Marion, 1883: 44.–Della Valle, 1893: 801, pl.3 fig.1, pl.27 figs 1-22 (in part).–Stebbing, 1906: 53.–Chevreux & Fage, 1925: 48, fig.30.–Chevreux, 1935: 36, pl.6 fig.4.– Cecchini & Parenzan, 1935: 163, fig.7.–Ruffo, 1946: 50.–*Nagata, 1965: 149.–*Nayar, 1966: 134.–*Griffiths, 1974: 309.–Krapp-Schickel, 1974: 322, 337.–*Griffiths, 1976: 56, 100, fig.31G.–Ledoyer, 1977: 374.–Diviacco & Ruffo, 1989: 488, figs 330, 331.–Palerud & Vader, 1991: 36.

Ichnopus affinis Heller, 1866: 19, pl.2 figs 19-25.–*Chevreux, 1895: 425.–Chevreux, 1903: 84.–Chevreux, 1935: 35.–Thurston & Allen, 1969: 359.–Krapp-Schickel, 1974: 322, 337.

Not *I. taurus*.–Walker, 1904: 238, pl.1 fig.3 (= *Ichnopus* sp.).

Not *I. taurus*.–K.H. Barnard, 1916: 123.

Not *I. taurus*.–Spandl, 1924: 43, fig.15 (= *I. serricrus*).

References marked with an asterisk are records which, because of their geographic location or depth, may represent species other than *I. taurus*. We have not examined the material.

We have examined the material of K.H. Barnard (1916) SAM A138 and it is not *I. taurus* because it has a long ischium and carpus on gnathopod 1. It therefore belongs in the *I. spinicornis* group. Unfortunately there are no mouthparts available and the material cannot be studied further.

Material examined. Female, 15 mm, Postillipo, Gulf of Naples, Mediterranean Sea, 40°46'N 14°14'E; male, 12 mm, AM P35699, Porto Caruso, north-western Ischia, Gulf of Naples, Mediterranean Sea, 40°45'N 13°50'E, 80 m, U. Schiecke, 29 Oct. 1969.

Diagnosis. Antenna 1: peduncular article 1 with short posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli in male only. Upper lip rounded. Mandible: left lacinia mobilis present; accessory spine row, left with 3, right with 4 spines; molar setose, weakly spinose; palp article 2 slightly broadened distally. Maxilla 1 with ST7 multicuspidate distally; palp inner margin distally serrate. Maxilliped: inner plate with 3 nodular spines; palp article 2 broad. Gnathopod 1: ischium and carpus very long; dactylus with long cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin minutely crenate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with moderate constriction.

Description. Based on female, 15 mm, AM P35698, and male, 12 mm, AM P35699. *Head*: slightly deeper than long, lateral cephalic lobe well developed, broadly rounded; rostrum absent; eyes reniform, very slightly enlarged in reproductive male. *Antenna 1:* medium length, about 0.2 times as long as body, 0.7 times as long as antenna 2; peduncular article 1 short, as long as broad, with short posterodistal tooth; accessory flagellum at least 5-articulate (male 10); callynophore, well-developed 2-field in female and male, with 5 small posterodistal setae; flagellum long, 30-articulate (male 35); calceoli present in reproductive male. *Antenna 2:* 0.4 times as long as body in female, 0.75 times as long as body in male; peduncle with brush setae in female and male, peduncular articles 4 and 5 not swollen in female or male; flagellum 40-articulate, (male 57-articulate); calceoli present in reproductive male.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded. *Mandible:* incisors symmetrical with slightly convex margins; left lacinia mobilis a small, slender spine; accessory spine row, left with 3 spines, right with 4 spines; molar setose with a few small spines distally; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, slightly broadened distally, with 6 (male 8) setae along distal third of medial margin and 7 setae on distolateral corner; article 3 slender, falcate, with 12 (male 15) proximal D-setae, and 4 short E-setae. *Maxilla 1:* inner plate small, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, weakly cuspidate, ST4 to ST6 large, slender, multicuspidate, ST7 short, multicuspidate distally, STA 1-cuspidate, STB to STD 2- to 3-cuspidate; palp large, 2-articulate, with 8 terminal spines and 1 flag seta. *Maxilla 2:* inner plate half length of outer plate. *Maxilliped:* inner plate large, subrectangular, with 3 well-developed nodular spines, oblique setal row reduced, with 9 plumose setae; outer plate medium size, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, submarginal setae vestigial; palp well developed, article 2 broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin

concave, forming slight anteroventrally produced corner; ischium very long, about 3.4 times as long as broad; carpus very long, 4.1 times as long as broad, 1.5 times as long as propodus; propodus long, subrectangular, 3.2 times as long as broad, margins subparallel; posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of medial spines and a row of 9 cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal in size to coxa 3; carpus long, 2.8

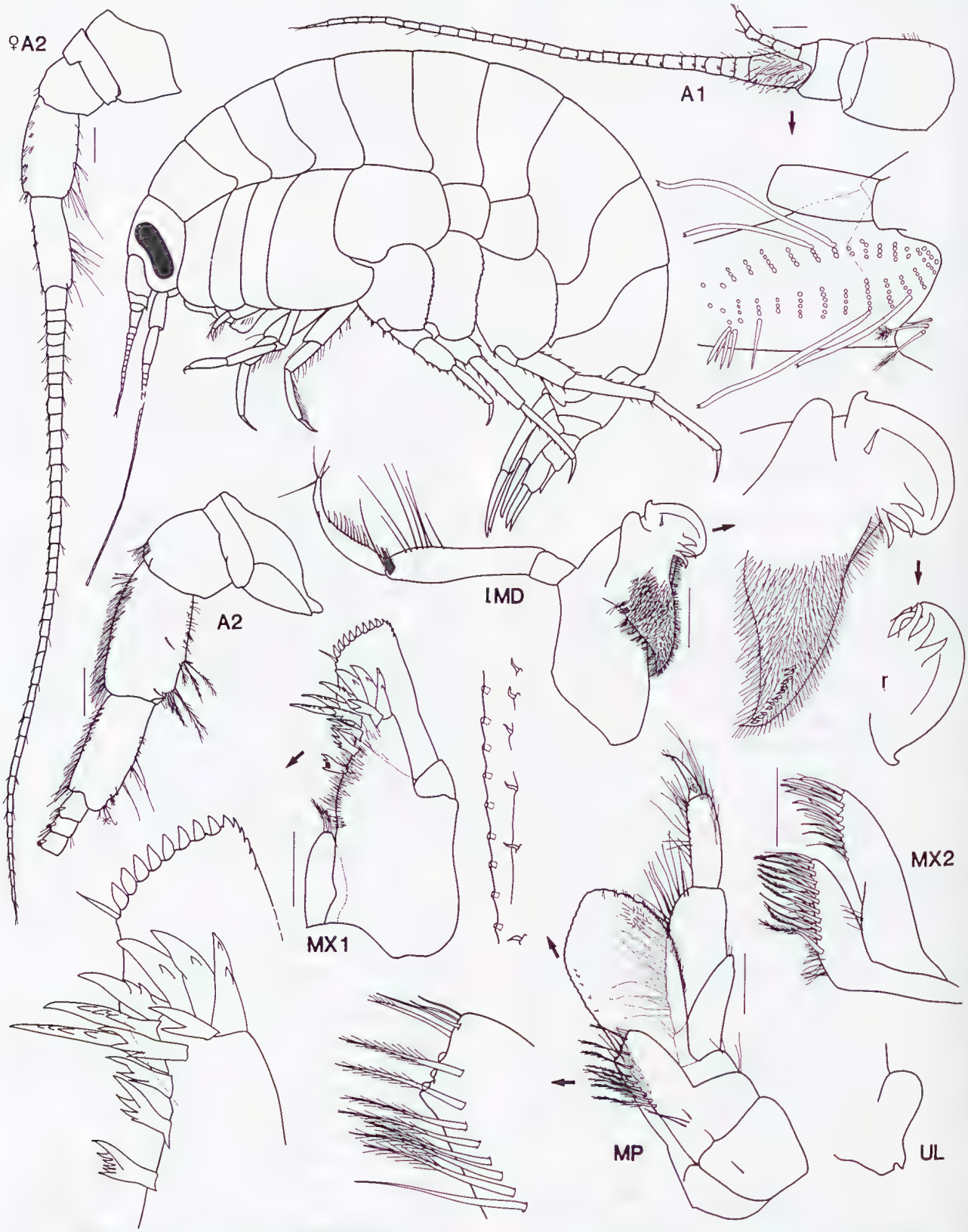

Fig.27. *Ichnopus taurus* Costa, female, 15 mm, AM P35698, male, 12 mm, AM P35699, Gulf of Naples, Mediterranean Sea. Scales represent 0.2 mm.

times as long as broad, posterior margin broadly lobate; propodus subovate, short, 1.6 times as long as broad; palm transverse, with straight, serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe, male merus/carpus with plumose setae. *Peraeopod 5:* coxa bilobate, anterior lobe slightly produced ventrally; basis expanded with posterior margin minutely crenate. *Peraeopod 7:* basis, posterior

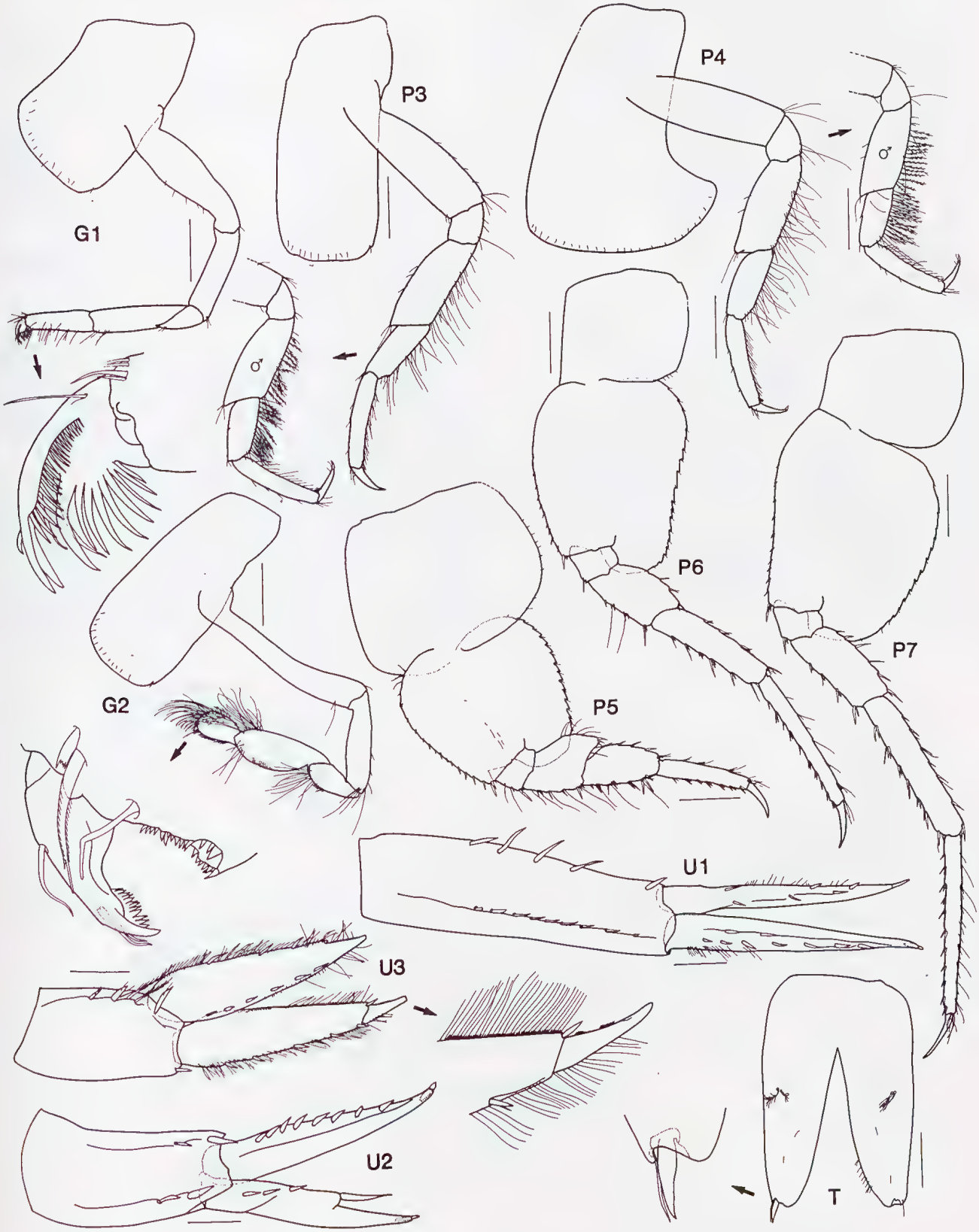

Fig.28. *Ichnopus taurus* Costa, female, 15 mm, AM P35698, male, 12 mm, AM P35699, Gulf of Naples, Mediterranean Sea. Scales for U1-3, T represent 0.2 mm, remainder represent 0.5 mm.

margin slightly rounded with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with small notch on posteroventral corner. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: with long fine setae; rami subequal in length, inner ramus with moderate constriction. *Uropod 3:* peduncle short, 1.75 times as long as broad without lateral flange; rami lanceolate, subequal in length with long fine setae and minutely serrate margins; plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (78%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. *Ichnopus taurus* appears at the base of the *I. taurus* species group. Its relationship to *I. macrobetomma* is not well understood, but it is considered to be the sister taxon of *Ichnopus* sp. (Walker, 1904, as *I. taurus*) from Sri Lanka. They are the only species in the group with a left lacinia mobilis, and along with *I. macrobetomma*, they are the only species in the group with a minutely crenate posterior margin on the basis of peraeopod 5. *Ichnopus taurus* differs from *Ichnopus* sp. in having a small posterodistal tooth on the first peduncular article of antenna 1 (lost in *Ichnopus* sp.), significantly more D-setae on mandibular palp article 3 and smaller spines on the mandibular molar. These minute differences probably reflect a recent vicariant event in the history of these animals, such as the closing of the Arabian Peninsula about 5 million years ago.

Distribution. *Ichnopus taurus* is known from the Mediterranean Sea, in depths of 50 to 400 m. Records from the Bay of Biscay, North Atlantic and the North Pacific Ocean probably represent other species.

Ichnopus tenuicornis (Haswell) new combination

Figs 29-31

Glycera tenuicornis Haswell, 1879a: 256, pl.8 fig.6.–Della Valle, 1893: 849.

Glycerina tenuicornis.–Haswell, 1882: 234, pl.4 fig.3.–Stebbing, 1906: 61.

? *Glycera tenuicornis*.–Haswell, 1879b: 322.

? *Glycerina tenuicornis*.–Stebbing, 1888: 643.–Whitelegge, 1889: 55.–J.L. Barnard, 1974: 141.

not *Glycerina tenuicornis*.–Pirlot, 1936: 271, figs 106, 107 (= *I. wardi*).

Haswell's original material of *Glycerina tenuicornis*, from the Howick Group, Great Barrier Reef, has been located among material from the Macleay Museum, University of Sydney, which was on loan to Keith Sheard at the time of Sheard's death. This material is now deposited in the Australian Museum, Sydney, and is described below.

As recorded by Barnard (1974) there is also a sample from Port Jackson. This sample (AM G5414) has been labelled as "Types". Since the original description gave only "Howick Group" as locality, the material from Port Jackson cannot be regarded as type material. The sample contains two partial specimens, in poor condition: one lacks the maxilliped and both sets of gnathopods; the other is an immature female with the entire head missing but with the enlarged palm of

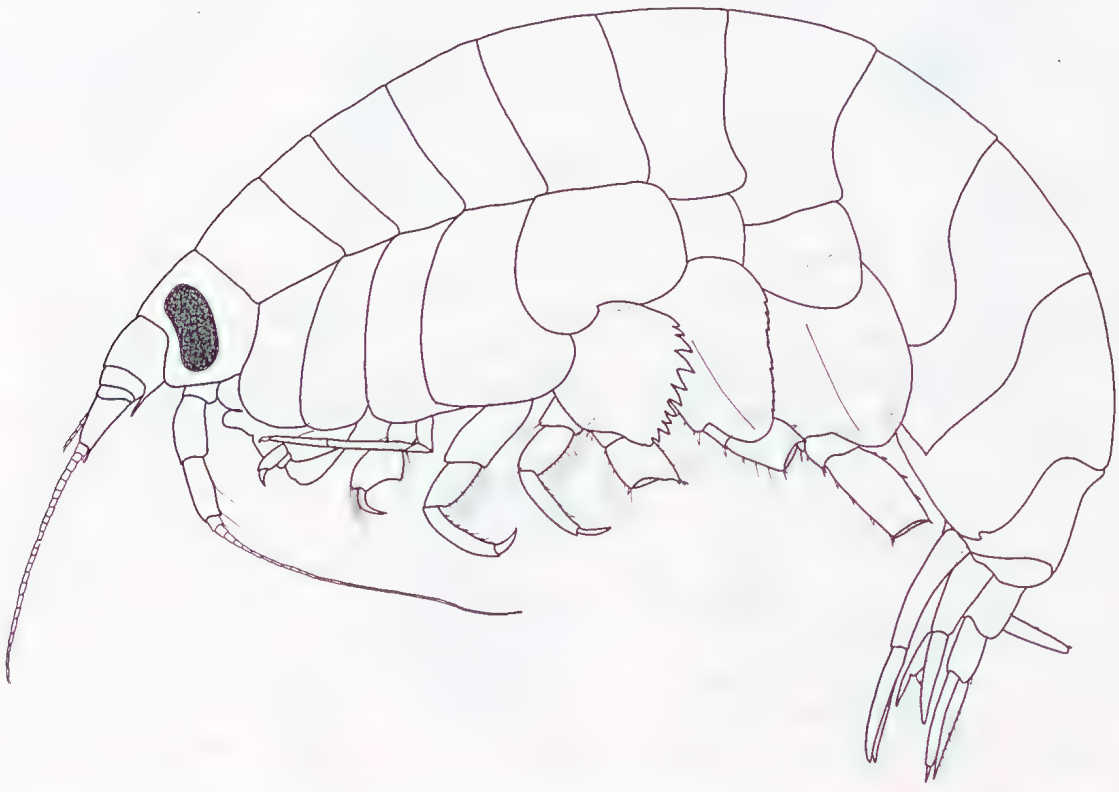

Fig.29. *Ichnopus tenuicornis* (Haswell), lectotype female, 10.5 mm, AM P39547, Howick Group, Great Barrier Reef, Australia.

gnathopod 2 described below for *I. tenuicornis*. It is not possible to identify with certainty either specimen, and recent collecting in Port Jackson has not yielded any specimens with an enlarged palm on gnathopod 2.

Type material examined. LECTOTYPE, female, 10.5 mm, non-ovigerous, AM P39547, PARALECTOTYPE, male, 9 mm, AM P39548, 10 PARALECTOTYPES, AM P39549, Howick Group, Great Barrier Reef, north-eastern Queensland,

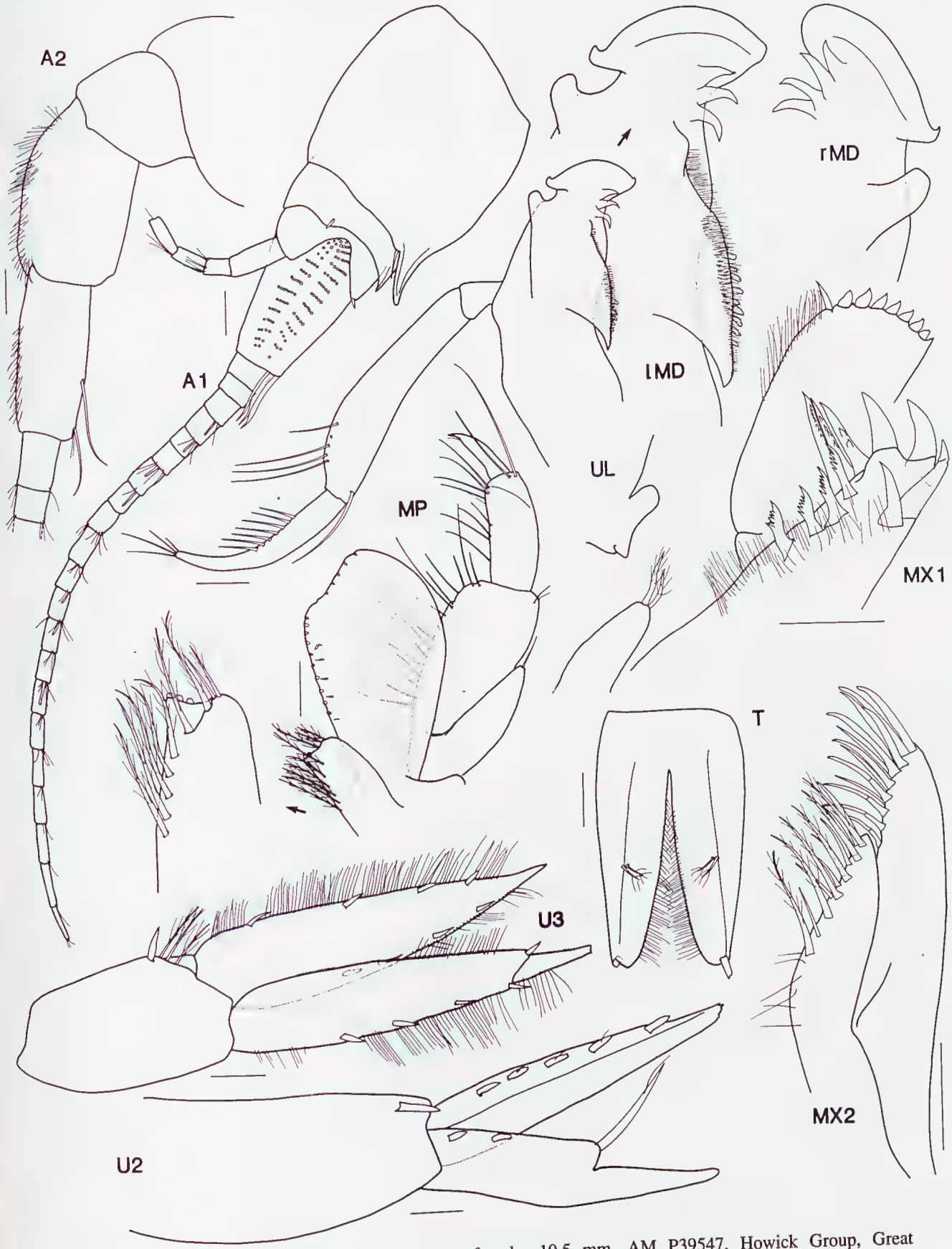

Fig.30. *Ichnopus tenuicornis* (Haswell), lectotype female, 10.5 mm, AM P39547, Howick Group, Great Barrier Reef, Australia. Scales represent 0.1 mm.

Australia, [approximately 14°29'S 144°55'E].

Additional material examined. 26 females, 35 males, 10 immature specimens, AM P39550 to P39584, 1 male, 1 female, BMNH 1990:36:2, 1 male, 1 female, USNM 253721, from 37 stations, North West Shelf, Western Australia, 19-20°S 117-119°E, epibenthic sled, 37-86 m, T. Ward for CSIRO on RV *Soela*, Dec. 1982-Oct. 1983; 3 specimens, AM P41014, west side of Oxley Island, Northern Territory, Australia, 11°00'S 132°49'E, muddy sand, 14 m, J.K. Lowry & G.C.B. Poore, 12 Oct. 1982, stns NT-85 and NT-88; 2 females, 1 male, AM P39587, off reef face between Bird Islet and South Island, Lizard Island, north Queensland, 14°40'S 145°28'E, baited trap at night on *Halimeda* beds, 30 m, J.K. Lowry & R.T. Springthorpe, 12 Feb. 1987, QLD-117; 1 juvenile, AM P39902, Mrs Watsons Bay, off Chinamans Ridge, Lizard Island, Queensland, baited trap on sand at night, 9-12 m, J.K. Lowry & R.T. Springthorpe, 15 Feb. 1987, QLD-119.

Diagnosis. Antenna 1: peduncular article 1 with long posterodistal tooth; callynophore with posterodistal spines. Antennae 1 and 2: calceoli in male only. Upper lip rounded. Mandible: left lacinia mobilis absent;

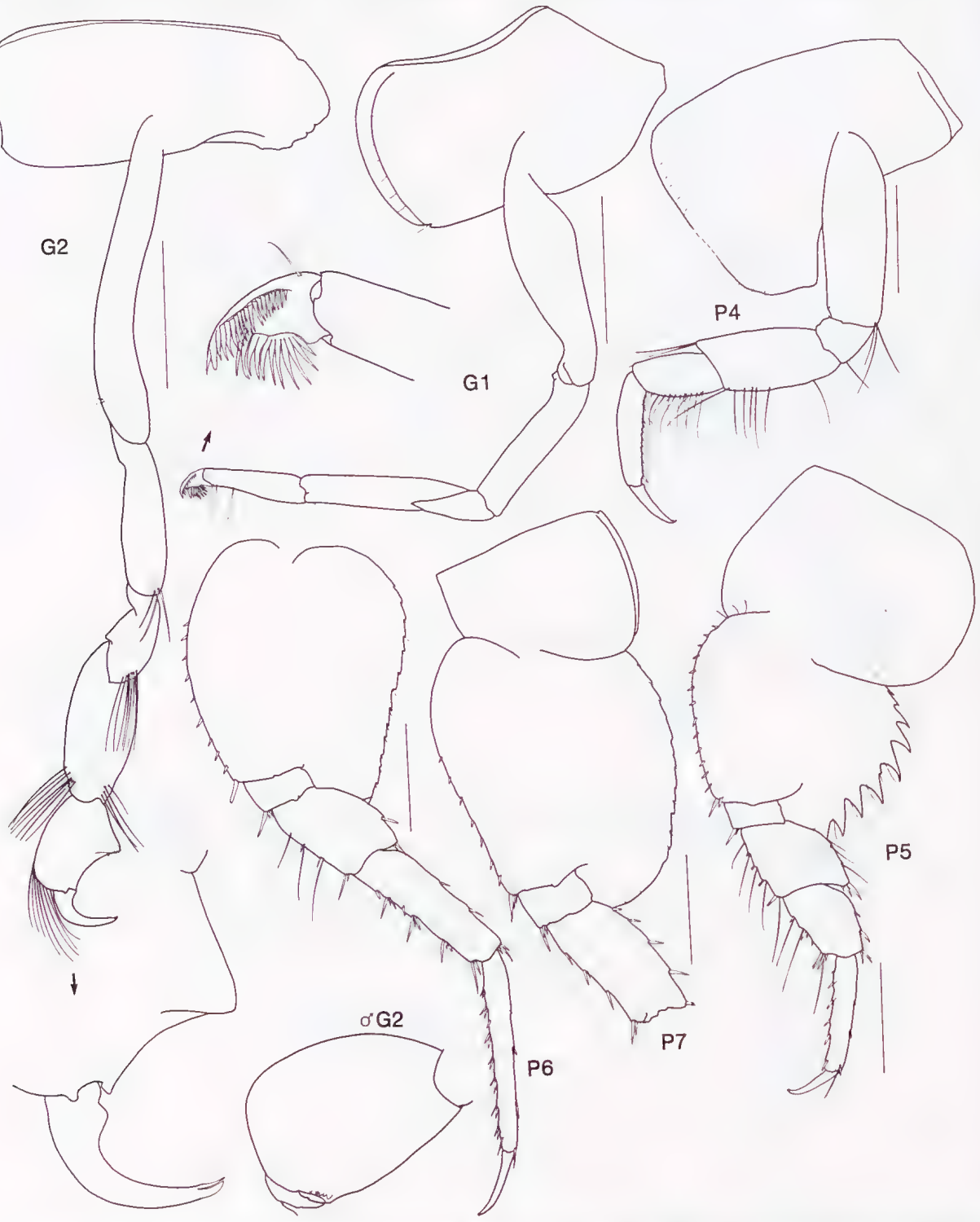

Fig.31. *Ichnopus tenuicornis* (Haswell), lectotype female, 10.5 mm, AM P39547, paralectotype male, 9 mm, AM P39548, Howick Group, Great Barrier Reef, Australia. Scales represent 0.5 mm.

accessory spine row, left with 2-4, right with 4-5 spines; molar setose, weakly spinose; palp article 2 slightly broadened distally. Maxilla 1 with ST7 multicuspidate distally; palp inner margin distally smooth. Maxilliped: inner plate with 3 nodular spines; palp article 2 very broad. Gnathopod 1: ischium and carpus very long; dactylus with long cuticular spines. Gnathopod 2: palm enlarged in female. Peraeopod 5: basis with posterior margin deeply serrate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with moderate constriction.

Description. Based on lectotype female, 10.5 mm and paralectotype male, 9 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, narrowly rounded; rostrum absent; eyes reniform, slightly enlarged in reproductive male. *Antenna 1:* medium length, about 0.2 times as long as body, 0.75 times as long as antenna 2; peduncular article 1 short, as long as broad, with long posterodistal tooth; accessory flagellum at least 4-articulate (male at least 6); callynophore, well-developed 2-field in female and male, with 3 posterodistal spines; flagellum long, 22-articulate (male 25); calceoli present in reproductive male. *Antenna 2:* about 0.3 times as long as body in female; flagellum 36-articulate, about 0.6 times as long as body in male (46-articulate); peduncle with brush setae in female and male, peduncular articles 4 and 5 not swollen in female or male; calceoli present in reproductive male.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, rounded. *Mandible:* incisors symmetrical, with slightly convex margins; lacinia mobilis absent; accessory spine row, left with 3 spines, right with 4 spines; molar setose, weakly spinose; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, slightly broadened distally (slightly more in male than female), with 5 (male 8) setae along distal third of medial margin, 4 setae on distolateral corner; article 3 slender, falcate, with 7 (male 9) proximal D-setae and 4 E-setae. *Maxilla 1:* inner plate small, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, without cusps, ST4 to ST6 large, slender, multicuspidate, ST7 short, multicuspidate distally, STA without cusps, STB to STD 4- to 5-cuspidate; palp large, 2-articulate, with 7 terminal spines and 1 flag seta. *Maxilla 2*: inner plate three quarters as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 3 well-developed nodular spines, oblique setal row reduced, with 9 plumose setae; outer plate large, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, submarginal setae vestigial; palp well developed, article 2 very broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium very long, about 4.5 times as long as broad; carpus very long, 5.7 times as long as broad, 1.7 times as long as propodus; propodus long, subrectangular, 3.3 times as long as broad, slightly tapering distally, posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of about 20 medial spines and a row of 11 long cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate, grossly subchelate in female; coxa large, subequal in size to coxa 3; carpus elongate, 2.2 times as long as broad, posterior margin broadly lobate; propodus subquadrate, short, 1.4 (male), 1.2 (female) times as long as broad; male palm acute, with slightly concave margin, female palm acute with enlarged concave margin guarded by a large blunt tooth.

Peraeopod 4: coxa with well-developed posteroventral lobe, anterior and posterior margins subparallel; male merus/carpus with plumose setae. *Peraeopod 5:* coxa bilobate, anterior lobe slightly produced ventrally; basis expanded with posterior margin deeply serrate. *Peraeopod 7:* basis, posterior margin slightly rounded with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

Epimeron 3: with small notch on posteroventral corner. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: with few long fine setae; rami subequal in length, inner ramus with moderate constriction. *Uropod 3:* peduncle short, 1.8 times as long as broad, without lateral flange; rami lanceolate, subequal in length with long fine setae and minutely serrate margins; plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (77%), without dorsal spines, distal margins rounded, with 1 spine on each margin.

Variation. *Ichnopus tenuicornis* shows some variation in the number of accessory spines on the mandible. The 9 mm paralectotype male has the usual 3 accessory spines on the left mandible, but 5 on the right. One adult male from the North West Shelf and a female from Lizard Island have 4 on both the left and right, and an adult male from Lizard Island has 2 on the left and 4 on the right. These specimens were not distinctive in any other character.

The enlarged palm of gnathopod 2 does not occur in juveniles or immature females.

Remarks. *Ichnopus tenuicornis* is a member of the *I. taurus* species group. Within this group it belongs to a group of four species (including *I. caritus*, *I. cribensis* and *I. parriwi*) which have spines instead of setae posterodistally on the callynophore. It differs from all species in this group in having the palm of gnathopod 2 enlarged in the female. In this regard it is similar to *I. woodmasoni*. But *I. woodmasoni* does not have a very long ischium and carpus on the first gnathopods. It differs from *I. parriwi* in not having calceoli in the female, from *I. caritus* in having spines on the mandibular molar and from *I. caritus* and *I. cribensis* in having a slightly expanded mandibular palp article 2.

Ichnopus tenuicornis appears to be a nocturnal scavenger. At Lizard Island it occurs in *Halimeda* beds on sand bottoms below 9 m.

Distribution. *Ichnopus tenuicornis* is a tropical species known from the North West Shelf of Western Australia, north of Cobourg Peninsula in the Northern Territory and the Great Barrier Reef of Queensland in depths of 9 to 86 m. One record of this species from Port Jackson cannot be substantiated.

Ichnopus teretis (Andres) new combination

Fig.32

Glycerina teretis Andres, 1981: 430, figs 1, 2.

Type material examined. HOLOTYPE male, SMF 9193 (as 1 slide) and PARATYPE female, SMF 9194b (as 1 slide), central Red Sea, 21°18.6'N 38°3.82'E, baited trap, 1869 m, Thiel & Türkay, 20 Oct. 1977, MESEDA I, stn So-02/50 FF.

Diagnosis. Antenna 1: peduncular article 1 with short posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli absent. Upper lip rounded. Mandible: left lacinia mobilis absent; accessory spine row, left with 3-4, right with 4 spines; molar setose, without spines; palp article 2 slender. Maxilla 1 with ST7 multicuspidate distally; palp inner margin distally serrate. Maxilliped: inner plate with 3 nodular spines; palp article 2 broad. Gnathopod 1: ischium and carpus very long; dactylus with long cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin deeply serrate. Epimeron 3: posteroventral corner without notch. Uropod 2: inner ramus with weak constriction.

Remarks. *Ichnopus teretis* is a member of the *I. taurus* species group. The relationship of *I. teretis* to *I. capricornus* is discussed under that species. *Ichnopus teretis* has been well described by Andres (1981). For comparison with descriptions of new species in this paper we add the following characters. *Antenna 1*: callynophore 2-field, with at least one posterodistal seta, no posterodistal spines. *Mandible*: molar setose, without spines. *Maxilla 1*: outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, weakly cuspidate, ST4 to ST6 large, slender, multicuspidate, ST7 short, multicuspidate distally, STA 2- to 3-cuspidate, STB to STD 4- to 5-cuspidate.

Distribution. Central Red Sea in 1869 m depth.

Ichnopus wardi n.sp.

Figs 33-35

?*Glycerina tenuicornis*.–Pirlot, 1936: 271, figs 106, 107.

Type material. HOLOTYPE, female, 12.5 mm (with 13 embryos), AM P39588, PARATYPE, male, 13.5 mm, AM P39589, PARATYPE, male, AM P39590, North West Shelf, Western Australia, 18°59.3'S 118°45.8'E to 18°59.1'S 118°46.0'E, epibenthic sled, 84 m, T. Ward for CSIRO on RV *Soela*, 7 Dec. 1982, Cruise 06, Stn B5S; PARATYPES, 2 females, 2 males, AM P39591, North West Shelf, Western Australia, 18°56.6'S 118°44.9'E to 19°57.1'S 118°45.0'E, epibenthic sled, 86-88 m, T. Ward for CSIRO on RV *Soela*, 7 Dec. 1982, Cruise 06, Stn B4S; PARATYPES, 3 females, 1 immature female, AM P39592, North West Shelf, Western Australia, 19°2.0'S 118°47.2'E to 19°1.7'S 118°47.1'E, epibenthic sled, 82 m, T. Ward for CSIRO on RV *Soela*, 7 Dec. 1982, Cruise 06, Stn B6S; PARATYPES, 1 male, 1 female, BMNH 1990:35:2, North West Shelf, Western Australia, 19°08.4'S 119°02.4'E to 19°08.6'S 119°02.7'E, epibenthic sled, 78 m, T. Ward for CSIRO on RV *Soela*, 11 Dec. 1982, Cruise 06, Stn B10S; PARATYPES, 1 male, 1 female, USNM 253722, North West Shelf, Western Australia, 19°03.0'S 119°00.6'E to 19°04.1'S 119°01.1'E, epibenthic sled, 78-80 m, T. Ward for CSIRO on RV *Soela*, 11 Dec. 1982, Cruise 06, Stn B11S.

Additional material examined. 43 specimens, AM P39593 to AM P39615, from 23 stations, North West Shelf,

Fig.32. *Ichnopus teretis* (Andres), paratype female, SMF 9194b, central Red Sea. Scales represent 0.1 mm.

Western Australia, 19-20°S 117-119°E, epibenthic sled and beam trawl, 40-84 m, T. Ward for CSIRO on RV *Soela,* Feb.-Oct. 1983; 5 specimens, NMV J19731 to J19733, North West Shelf, Western Australia, 19°39'S 116°22-43'E to 20°1'S 117°11-18'E, dredged, 46-48 m, G.C.B. Poore and H.M. Lew Ton on RV *Soela,* 2-11 June 1983, stns NWS-5, 33 & 48; 1 specimen, AM P39616, outer barrier, Horseshoe Reef, Bootless Inlet, Papua New Guinea, approx. 9°32'S 147°16'E, steep sand and shell slope at base of front face of reef, 30 m, S. Arnam, 28 Oct. 1980, stn PNG-19; 1 male, as 14 slides, ZMA 965-978, near Waigeo Island, Indonesia, 0°03.8'N 130°02.5'E, fine sand and broken shell, 141 m, 14 Aug. 1899, *Siboga* stn 152; 1 juvenile, as 6 slides, ZMA 980-985, off Donggala, Celebes, Indonesia, [approx. 0°40'S 119°44'E], grey mud, 36 m, 18-19 June 1899, *Siboga* stn 86; 1 specimen, ZMC, Kei Islands, Indonesia, [approx. 5°35'S 132°45'E], sand and coral, trawled, 85 m, 9 May 1922, Danish Expedition to the Kei Islands stn 53; 1 mature male, ZMC, off Jolo, Mindanao, Philippines, [approx. 6°04'N 121°00'E], hard bottom, 1 m, dredge, Th. Mortensen, 17 Mar. 1914.

Diagnosis. Antenna 1: peduncular article 1 with long posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli present in male and female. Upper lip acute. Mandible: left lacinia mobilis absent; accessory spine row, left and right each with 4 spines; molar setose, strongly spinose; palp article 2 strongly broadened distally. Maxilla 1 with ST7 multicuspidate medially; palp inner margin distally serrate. Maxilliped: inner plate with 2 nodular spines; palp article 2 very broad. Gnathopod 1: ischium and carpus long; dactylus with short cuticular spines. Gnathopod 2: palm minute in female. Peraeopod 5: basis with posterior margin deeply serrate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with strong constriction.

Description. Based on holotype female, 12.5 mm and paratype male, 13.5 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, narrowly rounded; rostrum absent; eyes reniform, slightly enlarged in reproductive male. *Antenna 1:* medium length, about 0.3 times as long as body, 0.56 times as long as antenna 2; peduncular article 1 short, about as long as broad, with long posterodistal tooth; accessory flagellum 10-articulate, article 1 slightly elongate, 0.2 times as long as flagellum; callynophore, well-developed 2-field in female and male, with posterodistal setae; flagellum long, 27-articulate (male 39); calceoli present in female and male. *Antenna 2:* about 0.6 times as long as body in female, 0.75 times as long as body in male; peduncle with brush setae in female and male, peduncular articles 4 and 5 not swollen in female or male; calceoli present in female and male.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, acute. *Mandible:* incisors symmetrical with slightly convex margins; left lacinia mobilis absent; accessory spine row, left and right each with 4 spines; molar setose, strongly spinose; mandibular palp attached midway; article 1 about twice as long as broad; article 2 elongate, strongly broadened distally, with 12 setae along distal third of medial margin, 8 setae on distolateral corner; article 3 slender, falcate, with 16 proximal D-setae and 4 short E-setae. *Maxilla 1:* inner plate small, narrow with 2 apical plumose setae; outer plate extremely narrow, with 11 spine-teeth in a 7/4 crown arrangement, ST1 to ST3 large, stout, without cusps, ST4 to ST6 large, slender, multicuspidate, ST7 large, multicuspidate medially, STA 3-cuspidate, STB to STD 4- to 5-cuspidate; palp large, 2-articulate, with 5 terminal spines and 1 flag seta. *Maxilla 2:* inner plate three quarters as long as outer plate. *Maxilliped:* inner plate large, subrectangular, with 2 well-developed nodular spines, oblique setal row reduced, with about 6 plumose setae; outer plate medium size, subovate, apical setae and spines absent, medial spines reduced in size, bead-shaped, 4 vestigial submarginal setae present; palp well developed, article 2 very broad, dactylus well developed, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, forming anteroventrally produced corner; ischium long, 2.3 times as long as broad; carpus long, 2.6 times as long as broad, 1.3 times as long as propodus; propodus long, subrectangular, 3 times as long as broad, tapering distally, posterior margin smooth, straight, without spines; dactylus with large subterminal tooth, a row of 27 medial spines and a row of 7 cuticular teeth along posterior margin. *Gnathopod 2:* minutely subchelate; coxa large, subequal in size to coxa 3; carpus

Fig.33. *Ichnopus wardi* n.sp., male, 12.0 mm, NMV J19733, North West Shelf, Western Australia.

long, 2.4 times as long as broad, posterior margin broadly lobate; propodus subrectangular, short, 1.6 times as long as broad; palm acute, with straight, minutely serrate margin.

Peraeopod 4: coxa with well-developed posteroventral lobe, anterior and posterior margins subparallel; male and female merus/carpus with plumose setae. *Peraeopod 5:* coxa equilobate; basis expanded with posterior margin deeply serrate. *Peraeopod 7:* basis, posterior margin slightly rounded with rounded posteroventral corner and straight posteroventral margin; merus slender, not expanded posteriorly.

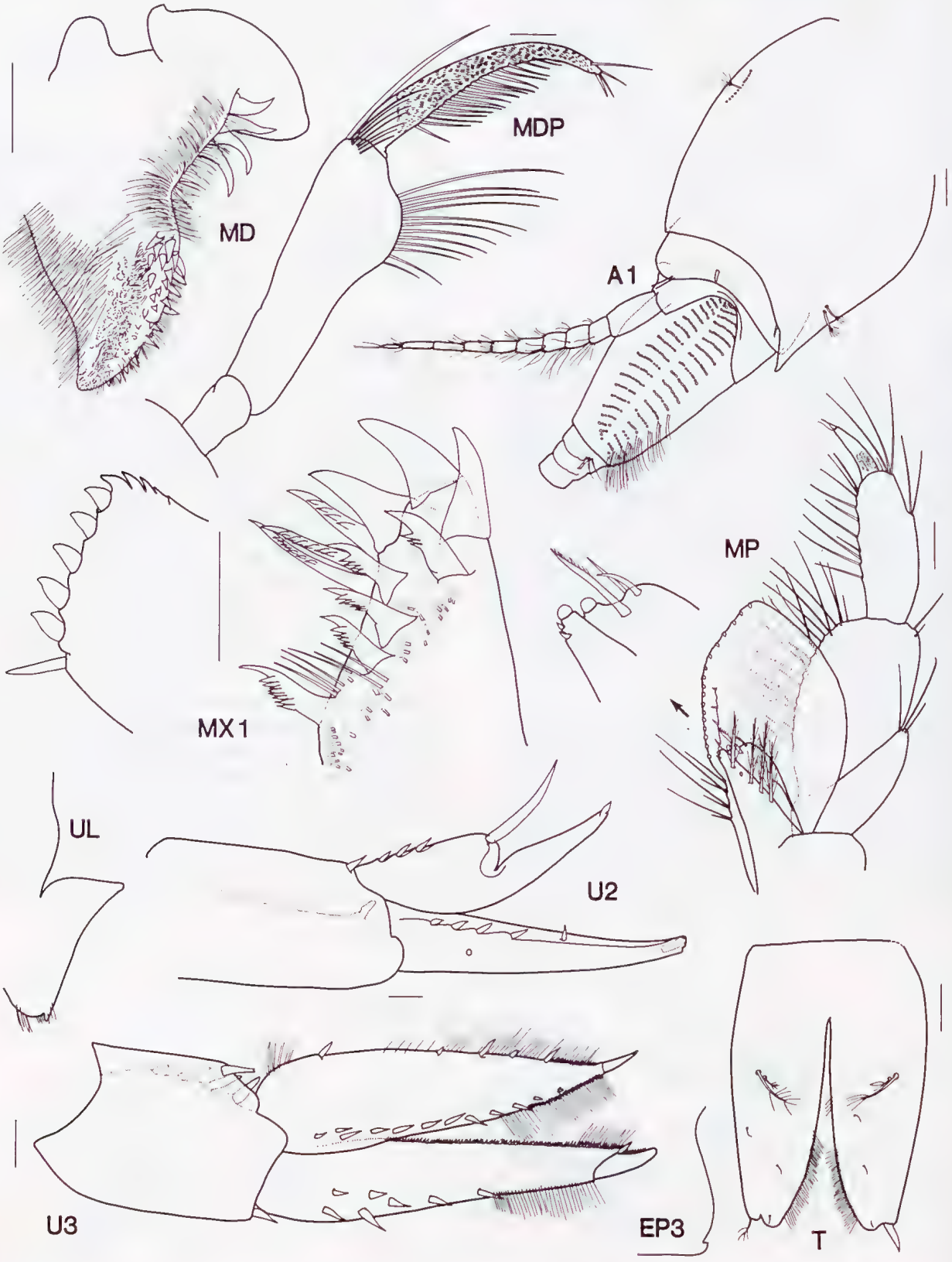

Fig.34. *Ichnopus wardi* n.sp., holotype female, 12.5 mm, AM P39588, North West Shelf, Western Australia. Scales represent 0.1 mm.

Epimeron 3: with small notch on posteroventral corner. *Uropod 1*: with long fine setae; rami subequal in length. *Uropod 2*: with few long fine setae; rami subequal in length, inner ramus with strong constriction. *Uropod 3:* peduncle short, 1.75 times as long as broad, without lateral flange; rami lanceolate, subequal in length; with long fine setae and minutely serrate margins, plumose setae absent in female and male; outer ramus 2-articulate. *Telson*: longer than broad, deeply cleft (74%), without dorsal spines, distal margins rounded, with 1 large spine on each margin.

Remarks. *Ichnopus wardi* is a peculiar member of the *I. spinicornis* species group. It differs from other members in having an acute upper lip (except *I. woodmasoni*) and a deeply serrate posterior margin (except *I. malpatun* and *I. woodmasoni*) on the basis of peraeopod 5. *Ichnopus wardi* differs from *I. woodmasoni* in having a minutely subchelate palm on the female gnathopod 2. Because *I. wardi* and *I. woodmasoni* can only be distinguished by the adult female, our identification of material from Indonesia and the Philippines is tentative. This material consists only of males and juveniles and its identification is based on

Fig.35. *Ichnopus wardi* n.sp., holotype female, 12.5 mm, AM P39588, North West Shelf, Western Australia. Scales represent 0.5 mm.

locality as much as morphology.

Etymology. This species is named after Dr Trevor Ward (CSIRO), who donated the North West Shelf amphipod collections to the Australian Museum.

Distribution. *Ichnopus wardi* is known from the North West Shelf, Western Australia; Bootless Inlet, Papua New Guinea and probably from Celebes, Waigeo Island and Kei Islands, Indonesia; and Jolo, Mindanao, Philippines; in 1 to 88 m depth.

Ichnopus woodmasoni (Giles) new combination

Figs 36-37

Lysianassa wood-masoni Giles, 1890: 68, pl.2 fig.4.
Lysianassa woodmasoni.–Stebbing, 1906: 88.–Thurston & Allen, 1969: 361.
Glycerina woodmasoni.–Barnard & Karaman, 1991: 488.

Type material examined. HOLOTYPE, female, 8 mm, BMNH 1968:53, Macpherson's Strait, Andaman Islands, Andaman Sea [approximately 11°30'N 92°40'E] dredged, coral sand bottom, 34 m, HMIMSS *Investigator*.

This specimen had remained, since Giles studied it, as a whole animal microscope mount. From the slide we were able to make a whole animal illustration and describe nearly all of the external morphology, but we could not describe the mouthparts or determine the sex. With the kind permission of Joan Ellis (BMNH) we were able to remove the specimen from the slide by dissolving the mounting medium with xylene. The specimen was in perfect condition and we were able to dissect (5 new slides) and illustrate it in detail. This remains the only collected specimen known.

Diagnosis. Antenna 1: peduncular article 1 with long posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli present in female, presumed present in male. Upper lip acute. Mandible: left lacinia mobilis absent; accessory spine row, left and right each with 4 spines; molar setose, strongly spinose; palp article 2 strongly broadened distally. Maxilla 1 with ST7 multicuspidate medially; palp inner margin distally serrate. Maxilliped: inner plate with 2 nodular spines; palp article 2 very broad. Gnathopod 1: ischium and carpus long; dactylus with short cuticular spines. Gnathopod 2: palm grossly subchelate in female, not known for male. Peraeopod 5: basis with posterior margin deeply serrate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus with strong constriction.

Description. Based on holotype, female, 8 mm; male not known. *Head and body*: colour semi-transparent. *Head*: deeper than long; lateral cephalic lobe large, narrowly rounded; rostrum absent; eyes reniform, colour deep purple. *Antenna 1*: medium length, 0.25 times body, peduncular article 1 short, length 1 times breadth, with long posterodistal tooth; peduncular article 2 short, 0.2 times article 1; accessory flagellum short, 0.3 times primary flagellum, 6-articulate, article 1 long, 2.7 times article 2; flagellum 17-articulate; callynophore strong 2-field in female, with some small posterodistal setae; calceoli present in female. *Antenna 2*: 0.36 times body length; peduncular article 3 short, 0.7 times article 4, peduncle with weak brush setae in female; peduncular articles 4 and 5 not enlarged in female; flagellum 30-articulate; calceoli present in female.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate, upper lip produced, acute; *Mandible*: incisors symmetrical, large, with slightly convex margins; left lacinia mobilis absent; accessory spine row, left and right with 4, short, slender, simple spines; molar a setose tongue, strongly spinose; mandibular palp attached midway; article 1 short, length 1.2 times breadth, without setae; article 2 elongate, strongly broadened distally, length 3.2 times breadth, 1.2 times article 3, with 5 setae on distal third of medial margin, and 4 setae near distal margin; article 3 slender, falcate, length 5.3 times breadth, with 6 proximal D-setae and 3 apical E-setae. *Maxilla 1*: inner plate narrow with 2 plumose apical setae; outer plate extremely narrow with 11 spine-teeth in 7/4 crown arrangement; ST1 to ST3 large, stout, without cusps, ST4 large, slender, 3-cuspidate, ST5 large, slender, 4-cuspidate, ST6 long, slender, multicuspidate, ST7 short, multicuspidate medially; STA large, displaced from STB-STD, 4-cuspidate, STB to STD short, slender, 4-cuspidate; palp large, 2-articulate, with 4 terminal spines; flag seta present on distolateral corner; distomedial margin serrate. *Maxilla 2*: inner and outer plates narrow; inner plate three quarters length of outer plate. *Maxilliped*: inner plate large, subrectangular, with 2 nodular spines, oblique setal row reduced with 2 plumose setae; outer plate medium size, subovate, without apical setae or spines, medial spines present, bead-shaped, submarginal setae vestigial; palp large, 4-articulate, article 2 very broad, length 1.8 times breadth, 1.5 times article 3; article 3 long, slender, length 2.1 times breadth, dactylus well developed, unguis present.

Gnathopod 1: simple, coxa large; anterior margin concave, anteroventral corner produced, posterior margin straight; basis long, slender, length 2.5 times breadth, with simple setae along anterior margin; ischium long, length 2.5 times breadth; carpus subrectangular, long, length 2.4 times breadth, 1.1 times as long as propodus; propodus large, subtriangular, length 2.75 times breadth, tapering distally, posterior margin smooth, straight, without spines, palm absent; dactylus complex, with large subterminal tooth, row of 18 medial spines and row of 5 short cuticular teeth along posterior margin. *Gnathopod 2*: grossly subchelate in female; coxa large, subequal in size to coxa 3; ischium long, length 3.8 times breadth; carpus long, length 2.8 times breadth, posterior margin broadly lobate; propodus subquadrate, short, length 1.4 times breadth, palm extremely acute, with concave, smooth margin, posterodistal corner without spines.

Peraeopod 3: coxa large; merus weakly expanded anteriorly; female merus-carpus with plumose setae. *Peraeopod 4*: coxa with large posteroventral lobe, anterior margin rounded, posterior margin sloping anteriorly; merus weakly expanded anteriorly; female merus-carpus with plumose setae. *Peraeopod 5*: coxa equilobate; basis expanded with posterior margin deeply serrate; merus expanded with rounded posterior margin. *Peraeopod 6*: coxa small; basis expanded posteriorly with minutely crenate posterior margin; merus expanded with rounded posterior margin. *Peraeopod 7*: basis expanded posteriorly, posterior margin slightly rounded, minutely crenate, posteroventral corner rounded, posteroventral margin straight; merus not expanded posteriorly.

Epimeron 3: posteroventral corner with small notch. *Uropod 1*: with long fine setae; peduncle with 7 dorsolateral, 1 apicolateral, 4 dorsomedial and 1 apicomedial spines; rami subequal in length, outer ramus with 4 lateral spines, inner ramus with 2 medial and 3 lateral spines. *Uropod 2*: with long fine setae;

Fig.36. *Ichnopus woodmasoni* (Giles), holotype female, 8 mm, BMNH 1968:53, Macpherson's Strait, Andaman Islands, Andaman Sea. Scales represent 0.1 mm.

peduncle with 1 apicolateral and 1 apicomedial spines; rami subequal in length, outer ramus with 4 dorsal spines, inner ramus with 2 proximal dorsal spines and 1 large spine above strong constriction. *Uropod 3*: peduncle short, length 1.6 times breadth, with 2 apicolateral and 1 apicomedial spines; rami lanceolate, subequal in length, with long fine setae; outer ramus 2-articulate, article 2 short, with 3 lateral spines, inner ramus with 4 medial and 3 lateral spines. *Telson*: 1.5 times as long as broad, deeply cleft (73%), without dorsal spines, distal margins rounded, with 1 marginal spine on each lobe.

Remarks. *Ichnopus woodmasoni* is most closely related to *I. wardi* and *I. malpatun*. It differs from both of these species in the reduced number of D-setae on

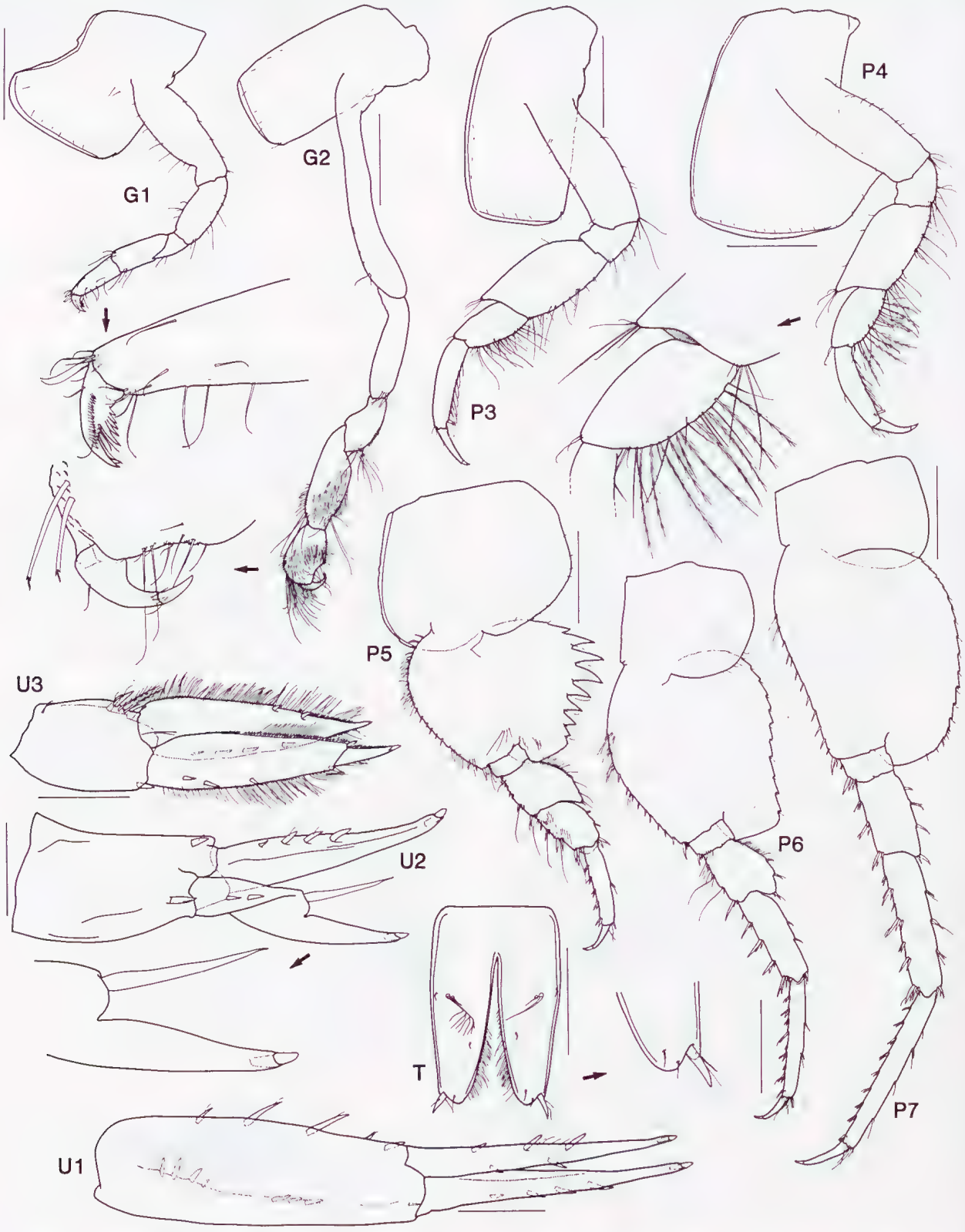

Fig.37. *Ichnopus woodmasoni* (Giles), holotype female, 8 mm, BMNH 1968:53, Macpherson's Strait, Andaman Islands, Andaman Sea. Scales represent 0.2 mm.

the mandibular palp and in the female gnathopod 2 which is grossly subchelate. It differs from *I. malpatun* in the acute upper lip.

Distribution. *Ichnopus woodmasoni* is known only from Macpherson's Strait, Andaman Islands, Andaman Sea in 34 m depth.

Ichnopus sp.

Fig. 38

Ichnopus taurus.–Walker, 1904: 238, pl.1 fig.3.

Material examined. One specimen, ?male, BMNH 1905.2.18:9 (carcass) and 1905.2.18:304 (1 slide), about 12 miles south of Galle, Sri Lanka (approximately 5°50'S 80°02.5'E), dredged with masses of calcareous branched and ramifying foraminiferal tubes (*Ramulina* sp.), about 200 m, W.A. Herdman and J. Hornell aboard S.S. *Lady Havelock*, 18 Feb. 1902, stn XLI.

Diagnosis. Antenna 1: peduncular article 1 without posterodistal tooth; callynophore with posterodistal setae. Antennae 1 and 2: calceoli present. Upper lip rounded. Mandible: left lacinia mobilis present; accessory spine row, left with 3, right with 4 spines; molar setose, weakly spinose; palp article 2 slender. Maxilla 1 with ST7 multicuspidate distally; palp inner margin distally serrate. Maxilliped: inner plate with 3 nodular spines, palp article 2 slender. Gnathopod 1: ischium and carpus very long; dactylus with long cuticular spines. Gnathopod 2: palm minute. Peraeopod 5: basis with posterior margin minutely crenate. Epimeron 3: posteroventral corner with small notch. Uropod 2: inner ramus not known.

Description. *Head*: deeper than long; lateral cephalic lobe large, broadly rounded; rostrum absent; eye shape not known. *Antenna 1*: medium length, peduncular article 1 short, length subequal to breadth, without posterodistal tooth; accessory flagellum short, 6-articulate, article 1 long, 2 times article 2; flagellum 39-articulate; callynophore strong 2-field, with 3 small posterodistal setae; calceoli present. *Antenna 2*: not known.

Mouthpart bundle: subquadrate. *Epistome* and *upper lip*: separate: upper lip produced, rounded; *Mandible*: incisors symmetrical, large, with slightly convex margins; left lacinia mobilis a small spine; accessory spine row, left with 3, right with 4 short, slender, simple spines; molar a setose tongue, moderately spinose; mandibular palp attached midway, article 1 short, without setae, article 2 elongate, slender, length 4.2 times breadth, 1.2 times article 3, with 3 setae on distal third of medial margin and 3 setae near distal margin, article 3 long, slender, falcate, length 5.5 times breadth, with 4 proximal D-setae and 4 apical E-setae. *Maxilla 1*: inner plate narrow with 2 plumose apical setae; outer plate extremely narrow with 11 spine-teeth in 7/4 crown arrangement; ST1 to ST3 large, stout, weakly cuspidate, ST4 large, slender, 3-cuspidate, ST5 large, slender, 4-cuspidate; ST6 large, slender, multicuspidate; ST7 short, multicuspidate distally, STA large, slightly displaced from STB-STD, 1 or 2-cuspidate, STB to STD 2- to 3-cuspidate; palp large, 2-articulate, with 5-6 terminal spines; flag seta present on distolateral corner; distomedial margin serrate. *Maxilla 2*: not known. *Maxilliped*: inner plate subrectangular with 3 nodular spines, oblique setal row reduced with 2 plumose setae; outer plate subovate, without apical setae or spines, medial spines vestigial, submarginal setae vestigial; palp large, 4-articulate, article 2 broad, length 2.2 times breadth, 1.4 times article 3; article 3 long, slender, length 2.5 times breadth; dactylus well developed, with 2 subterminal setae, unguis present.

Gnathopod 1: simple; coxa large, anterior margin concave, anteroventral corner produced, posterior margin straight; basis long, slender, length 3.9 times breadth, without setae along anterior margin; ischium very long, length 4 times breadth; carpus subtriangular, long, length 3.75 times breadth, 1.25 times as long as propodus; propodus large, subrectangular, length 3.5 times breadth, margins subparallel, posterior margin smooth, straight; dactylus complex, with large subterminal tooth, row of 19 medial spines and row of 6 long cuticular teeth along posterior margin. *Gnathopod 2*: minutely subchelate; coxa large, subequal in size to coxa 3; ischium long, length 3.4 times breadth; carpus long, length 2.5 times breadth, posterior margin broadly lobate; propodus subquadrate, short, length 1.3 times breadth; palm acute, with concave, smooth margin, posterodistal corner without spines.

Peraeopods 3-4, 6-7: not known. *Peraeopod 5*: basis expanded with posterior margin minutely serrate; merus expanded with straight posterior margin; propodus with 5 spines and 1 distal pair of locking spines along anterior margin; dactylus long, slender.

Oostegites: not known. *Gills*: not known.

Epimeron 3: posteroventral corner strongly notched. *Uropods 1 to 3*: not known. *Telson*: longer than broad, deeply cleft, without dorsal spines, distal margins truncated, with 1 marginal spine on each lobe.

Remarks. This species was originally reported by Walker (1904) as *Ichnopus taurus*. Although the peraeopods and uropods no longer exist it is possible from the remaining parts to determine that it is an undescribed species closely related to *I. taurus*. The differences between the two taxa are discussed under *I. taurus*.

Distribution. This species is known from the benthic shelf off Sri Lanka in about 200 m depth.

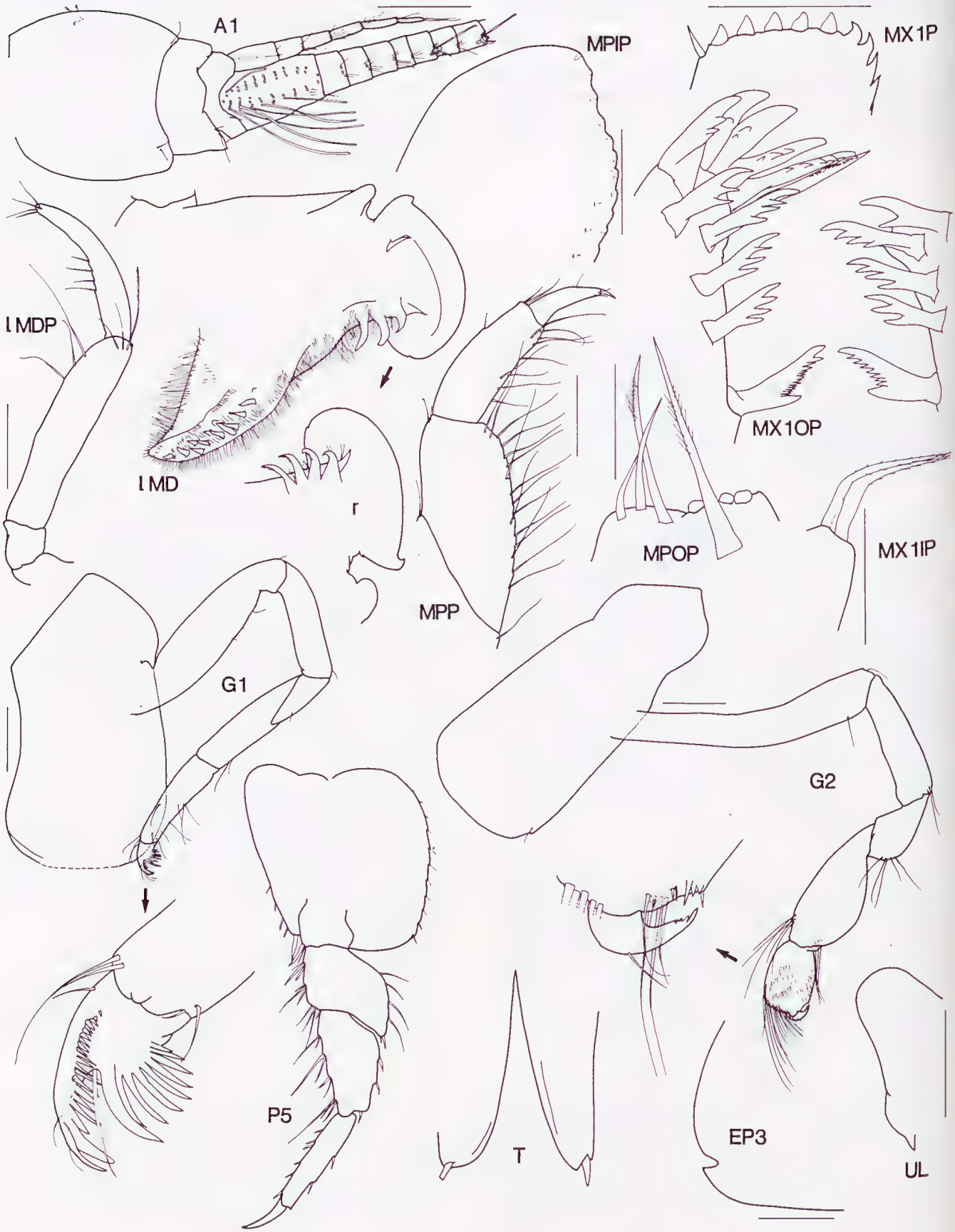

Fig.38. *Ichnopus* sp., ?male, BMNH 1905.2.18:9 and 1905.2.18:304, south of Galle, Sri Lanka. Scales for MX1IP, MPIP represent 0.05 mm; for E, G1-2, EP3 represent 0.2 mm; remainder represent 0.1 mm. P5 after Walker, 1904.

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Description of a New Dottyback of the Genus *Pseudochromis* (Pisces: Pseudochromidae) from Western Australia

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ABSTRACT. A new species of *Pseudochromis* (Pseudochromidae) is described on the basis of a single specimen trawled from 80 m at Glomar Shoal, off northern Western Australia. *Pseudochromis reticulatus* n.sp. is separable from other *Pseudochromis* in having the following characters in combination: dorsal rays III,27 (all soft rays branched), anal rays III,15, scales in lateral series 34 to 36, anterior lateral line scales 28 to 30, circumpeduncular scales 16, and caudal fin pointed.

GILL, A.C. & D.J. WOODLAND, 1992. Description of a new dottyback of the genus *Pseudochromis* (Pisces: Pseudochromidae) from Western Australia. Records of the Australian Museum 44(3): 247–251.

The coral reef fish family Pseudochromidae is currently divided into four subfamilies (Godkin & Winterbottom, 1985): Pseudochrominae (with nearly 70 species), Pseudoplesiopinae (about 25 species), Anisochrominae (2 species) and Congrogadinae (19 species). Studies of material for a systematic revision of the Pseudochrominae by the senior author have resulted in the discovery of a single specimen representing a new species.

This paper presents a description of the new species, which is here assigned tentatively to the genus *Pseudochromis* Rüppell (1835). Until recently, only one other pseudochromine genus, *Labracinus* Schlegel (1858), has been generally recognised. Cladistic studies of osteological and other characters by the senior author have provided evidence for the resurrection of *Assiculus* Richardson (1846), *Cypho* Myers (1940 = *Nesiotes* De Vis, 1884) and *Ogilbyina* Fowler (1931) from synonymy with *Pseudochromis*, and the recognition of three new genera (all based on species previously referred to *Pseudochromis*). *Pseudochromis*, with over two thirds of the pseudochromine species, still remains a 'wastebasket' for species which cannot be placed in the other genera. More definite placement of the new species must await the completion of osteological studies which are being pursued in order to refine the generic classification of

the Pseudochrominae.

Methods and Materials

All measurements to the snout tip were to the midanterior of the snout. Standard length (SL) was measured from the snout tip to the middle of the caudal fin base at the vertical through the posterior edge of the dorsal hypural plate. Head length was measured from the snout tip to the dorsal edge of the gill opening with the calipers fitting relatively tightly. Snout length was measured over the shortest distance from the snout tip to the orbital rim without constricting the fleshy margin of the latter. Orbit diameter was measured as its fleshy horizontal length. Predorsal, prepelvic and preanal lengths were measured from the snout tip to the base of the first spine of the relevant fin. Body width was measured at the (post-temporal) pore patch immediately dorsoanterior to the upper edge of the gill opening. Caudal peduncle length was measured from the posterior edge of the base of the last anal fin ray to the ventral edge of the caudal peduncle at the vertical through the posterior edge of the ventral hypural plate. Caudal peduncle depth was measured obliquely between the bases of the last dorsal and last anal fin rays. Measurements of fin elements excluded any filamentous membranes. Caudal fin length was the length of the lowermost of the rays on the upper hypural plate.

The last ray in the dorsal and anal fins is divided at its base and was counted as one ray. The upper ray in the pectoral fins is rudimentary and rotated so that the asymmetrical medial and lateral segments appear to represent two separate rays; these were counted as a single ray. Counts were made of the scales in the dorsoanterior ('anterior') and midlateral ('posterior') lateral lines, and included intermittent non-tubed scales and empty scale pockets. The posterior lateral line count was partitioned into a peduncular (ending with the scale at the hypural margin) and a caudal fin component. Scales in lateral series was defined as the number of scales in the anterior lateral line plus the number of transverse scale rows on the caudal peduncle, the latter count beginning with the transverse row following the last tubed scale in the anterior lateral line and finishing with the transverse row passing through the mid-posterior edge of the hypural plate. Two counts of cheek scales rows were made, one ('scales behind eye') of the vertical rows from the midposterior edge of the orbital rim to the upper edge of the preopercle, the other ('scales to preopercle angle') of the oblique rows from the posteroventral orbital rim to the preopercle angle. Gill raker counts included all rudiments; the angle raker was included in the lower (second) count. Circumorbital pores were counted from the first anterior interorbital pore (the bilateral pore behind the pore immediately dorsoposterior to the posterior nostril) around the orbital rim to the pore associated with the terminal opening of the first infraorbital bone (= lachrymal) (the pore immediately below the posterior nostril). Counts of preopercular pores were of all pores associated with the preopercle, including those associated with the terminal openings. Posterior interorbital pores are unpaired, median pores positioned in between and usually slightly posterior to the paired (anterior) interorbital pores. Osteological details are based on a radiograph. Other counts and measurements are standard (Hubbs & Lagler, 1958).

Where meristic values were recorded bilaterally, the two counts are separated by a slash; the first value given is the left count. Patterns of insertion of supraneural bones and anterior dorsal fin pterygiophores between neural spines are given as a predorsal formula following Ahlstrom *et al.* (1976). A preanal formula depicting the pattern of insertion of anal fin pterygiophores is also given, where the first slash represents the first haemal spine (i.e., haemal spine of vertebra 11). The holotype is deposited in the Northern Territory Museum, Darwin (NTM).

Pseudochromis reticulatus n.sp.

Figs 1,2

Material examined. HOLOTYPE, NTM S.10821-004, 50.7 mm SL, Western Australia, Glomar Shoal (19°32'S 116°48'E), 80 m, Northern Territory Fisheries, 19 Sept. 1982.

Diagnosis. *Pseudochromis reticulatus* is distinguished from all other pseudochromids in having the following combination of characters: dorsal fin rays III,27, all soft rays branched; anal fin rays III,15; scales in lateral series 34-36; anterior lateral line scales 28-30; circumpeduncular scales 16; second anal fin spine only marginally stouter than third; caudal fin pointed; colour in preservative generally pale pinkish brown, dorsal contour of body with dark greyish-brown reticulations surrounding large pale spots at the base of each scale.

Description. Dorsal fin rays III,27, all soft rays branched; anal fin rays III,15, all soft rays branched; pectoral fin rays 18/19 (upper 2/1, lower 1/2 rays simple, remaining rays branched); pelvic fin rays I,5, all soft rays branched; branched caudal fin rays 8+7; upper procurrent caudal fin rays 6; lower procurrent caudal fin rays 6; scales in lateral series 36/34; anterior lateral line scales 30/28; anterior lateral line terminating beneath dorsal fin soft ray 24/22; peduncular lateral line scales 7/7; caudal fin lateral line scales 1/0; horizontal scale rows between anterior and posterior lateral lines 3/3; horizontal scale rows above anal fin origin 14+1+2/13+1+2; predorsal scales 18; circumpeduncular scales 16; scales behind eye 2/2; scales to preopercle angle 5/5; circumorbital pores 25/24; preopercular pores 12/10; dentary pores 4/4; posterior interorbital pores 1; gill rakers 5+13; pseudobranch lobes 10.

As percentage of SL: head length 23.5; predorsal length 33.1; prepelvic length 33.1; preanal length 59.2; dorsal fin base 60.0; anal fin base 25.4; dorsal fin origin

to pelvic fin origin 26.4; anal fin origin to middle dorsal ray (spines included in ray count) 25.0; snout length 6.1; orbit diameter 10.1; body width 13.0; fleshy interorbital width 5.7; bony interorbital width 3.7; snout tip to retroarticular tip 14.8; caudal peduncle length 13.6; caudal peduncle depth 16.2; first dorsal spine length 3.4; second dorsal spine length 5.9; third dorsal spine length 8.3; first dorsal soft ray length 12.6; fourth last dorsal soft ray length 19.5; first anal spine length 2.0; second anal spine length 4.9; third anal spine length 7.3; first anal soft ray length 11.8; fourth last anal soft ray length 15.2; third pectoral ray length 15.8; pelvic spine length 11.2; second pelvic soft ray length 24.3; caudal fin length 34.7.

Lower lip incomplete, with broad interruption at symphysis; dorsal and anal fins without basal scale sheaths; predorsal scales extend anteriorly to second anterior interorbital pore; operculum with 5 irregular, small, indistinct serrations; denticles of outer ceratobranchial 1 gill rakers well developed on raker tips only; predorsal formula 0/0/0+2/1+1/1/1/1/1+1; dorsal fin spines pungent and relatively stout; preanal formula 2/1+1/1/1+1/1/1+1; anal fin spines pungent and relatively stout, the second spine only marginally stouter than the third; pelvic fin spine pungent and moderately stout; second pelvic soft ray longest; caudal fin pointed (rounded, with middle rays extended); vertebrae 10+16; epipleural ribs 14.

Colouration. Live colouration unknown. Preserved colouration: head and body pale pinkish brown becoming slightly darker posteriorly; scattered greyish brown pigment forming an indistinct stripe from behind eye to branchial opening; stripe contacting a less distinct short, curved streak extending around ventroposterior orbital rim; dorsal contour of caudal peduncle and body excluding predorsal contour and nape dark grey-brown; scales of dark area of body each with a large, pale basal

Fig.1. Holotype of *Pseudochromis reticulatus*, NTM S.10821-004, 50.7 mm SL, Glomar Shoal, Western Australia.

Fig.2. Diagram of the head of *Pseudochromis reticulatus* showing the distribution of cephalic lateralis pores. Arrow indicates anterior termination of predorsal scales.

spot (forming, in combination with background colouration, dark reticulations), these continuing ventrally onto pale area of body but becoming less distinct; dorsal fin white anteriorly on spinous portion, dusky hyaline posteriorly; each inter-radial membrane behind second soft ray with a short, dark grey-brown basal oblique stripe, these becoming indistinct posteriorly; anal fin dusky grey; caudal fin dusky brown with whitish upper and lower borders; pectoral and pelvic fins hyaline.

Remarks. The specific name *reticulatus* is from the Latin meaning netted or net-like and refers to the pattern of dark markings on the dorsum of the holotype. The gender is masculine.

Pseudochromis reticulatus is known only from the holotype trawled in relatively deep water (80 m) at Glomar Shoal off Western Australia. The range of the species is almost certainly more extensive, although the majority of pseudochromids have relatively narrow distributions when compared with other marine fishes (e.g., only one of seven Red Sea *Pseudochromis* ranges south into the Gulf of Aden). Other pseudochromins are relatively cryptic in behaviour, being closely associated with rock and/or coral reefs; the new species is probably no exception. The obvious logistic problems associated with collecting active, cryptic species at depths greater than about 50 or 60 m no doubt contribute heavily to the lack of further specimens of the species, despite, for example, recent demersal trawling at appropriate depths off north-western Australia by CSIRO Fisheries and Oceanography.

Determination of the relationships of *Pseudochromis reticulatus* to other species is at present difficult owing to the poor understanding of the osteology of the species (at present restricted to the few details which can be discerned either from an radiograph of the holotype or from external examination) and to the general confusion of relationships within *Pseudochromis*. However, it is possibly most closely related to a group of species including *P. andamanensis* Lubbock (1980), *P. marshallensis* Schultz (1953), *P. pylei* Randall & McCosker (1989) and at least two undescribed species from throughout the eastern Indian and western Pacific Oceans. Species of this 'complex' – which may not be monophyletic – are characterised by the following: outer ceratobranchial 1 gill rakers with well-developed denticles on raker tips only, all or most dorsal soft rays branched in adults, and a preserved colour pattern consisting of pale spots (one per scale; yellow, orange or red in life) at least dorsally on the body. *Pseudochromis reticulatus* is readily distinguished from all of these species in having 27 dorsal soft rays (versus 24-26 in the remaining species, although rarely 27 in *P. marshallensis* which otherwise has a strongly modal count of 25), second anal spine only marginally stouter than third (versus usually much stouter) and a pointed caudal fin (versus rounded, truncate or emarginate).

The new species may possibly be confused in the field with *Pseudochromis quinquedentatus* McCulloch (1926), which is also known from trawled specimens from off the coast of north-western Australia. However, *P. quinquedentatus* is readily distinguished in having a rounded to truncate or emarginate caudal fin (depending on the size of the specimen), several large conspicuous opercular serrations, anterior heads of the palatine tooth patches directed medially behind the posterolateral arms of the vomerine tooth patch (versus more-or-less in line with the posterolateral arms in *P. reticulatus*), and a colour pattern consisting of dark grey or brown scale spots dorsally on the anterior part of the body and the nape.

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New Desid Spiders (Araneae: Desidae) from New Caledonia and Eastern Australia

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ABSTRACT. Two related desid spider genera, *Canala* n.gen. from New Caledonia and *Colcarteria* n.gen. from eastern Australia, are described. *Epimecinus magnus* Berland, the type species of *Canala*, is diagnosed and figured. *Epimecinus longipes* Berland is removed from synonymy with *E. magnus* and referred to *Canala*. Its male is described. Newly described species are *Canala poya*, *Colcarteria carrai*, *C. yessabah* and *C. kempseyi*. The desine species *Forsterina koghiana* n.sp. from New Caledonia is described.

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Berland (1924) described six 'dictynid' species from New Caledonia in the genera *Epimecinus* Simon 1908, *Aphyctoschaema* Simon 1902 and *Syrorisa* Simon 1908. Lehtinen (1967) erected two genera, *Baiami* Lehtinen and *Forsterina* Lehtinen, into which he placed four of these species, two as synonyms (*E. magnus* Berland 1924, and its putative synonym *E. longipes* Berland 1924, in *Baiami*; *S. alticola* Berland 1924 and its synonym *A. alacris* Berland 1924 in *Forsterina*). Lehtinen (1967) placed *E. magnus* in *Baiami* (family Stiphidiidae), but Gray (1981) redefined *Baiami* as a southern Australian genus and excluded *E. magnus*. *Canala* n.gen., restricted to New Caledonia, is erected here for *E. magnus* and related species. These include *E. longipes*, which is removed from synonymy with *E. magnus*.

A related genus, *Colcarteria* n.gen., from northern New South Wales shares with *Canala* a distinctive combination of male palpal and female genitalic characters. These include the large, curved, basal median apophysis, the origin and course of the embolus, laminate and pointed retrolateral/ventral tibial apophyses, simple receptaculate genitalia with short, diverticulate insemination ducts and lateral teeth on the epigynum. *Canala* and *Colcarteria* are tentatively allocated to the family Desidae but affinities are apparent also with the Agelenidae and Stiphidiidae (*sensu* Forster 1970, Forster & Wilton 1973).

Berland (1924) recorded both *Forsterina alticola* (Berland) and its synonym, *A. alacris* Berland, from Mont Pani in northern New Caledonia. A new species described here comes from Mont Koghi in the south. While these spiders have clear affinities with the Australian *Forsterina* fauna and the related New Zealand genus *Reinga* Forster & Wilton 1973, a full revision of the genus *Forsterina* (Gray, in preparation) will determine if separate generic status is appropriate for the New Caledonian fauna.

All measurements are in millimetres. Colour pattern comments refer to alcohol preserved specimens. Description abbreviations: CL, CW – carapace length, width; AL, AW – abdomen length, width; EGW – eye group width; MOQL, MOQAW, MOQPW – median ocular quadrangle length, anterior width, posterior width; ML – maxilla length; LL, LW – labium length, width; SL, SW – sternum length, width; ALS, PMS, PLS – anterior lateral, posterior median and posterior lateral spinnerets. Repository abbreviations: AM – Australian Museum, Sydney; MNHN – Muséum National d'Histoire Naturelle, Paris; SAM – South Australian Museum, Adelaide.

Desidae

Canala n.gen.

Baiami.–Lehtinen 1967 (part): 218, 331.

Type species. *Epimecinus magnus* Berland 1924.

Etymology. The generic name refers to Mont Canala, the locality from which the type species was collected.

Diagnosis. Small-medium sized cribellate spiders. Caput prominent. Chelicerae long, more or less geniculate basally; groove long with 2 small, very widely spaced retromarginal teeth (basal tooth very small). Male palp with a large, sickle-shaped median apophysis, tibia with 2-3 retroventral laminate/pointed apophyses. Epigynum with lateral teeth. Receptacula contiguous, ducts directed laterally with small diverticula.

Description. Small-medium sized cribellate spiders (CL 1.5-5). Carapace with grey-brown cervical bands converging at the fovea (Y-shaped), marginal thoracic bands, eye region usually dark grey, dorsal abdomen grey-brown with paler anterior stripe and lateral spots coalescing posteriorly into chevrons, legs banded (pigmentation reduced in cavernicolous populations). Carapace strongly arched, with a prominent caput. Fovea slit-like. From above AER straight to slightly recurved, PER slightly recurved; frontally AER straight, PER procurved. AME smallest. Chelicerae robust, long, more or less geniculate basally, with a strong carina. Fang groove long, oblique; promargin with 7-15 teeth; retromargin with 2 small very widely separated teeth, apical tooth placed toward midline of groove, basal tooth very small or minute-absent and placed behind level of basal prolateral tooth. Labium and maxillae long, labium notched basolaterally and apically. Sternum cordate, extended posteriorly between coxae IV. Legs 1423, moderately long (leg I 4-5 times length carapace); trochanters notched. Legs I,II ventral spines - tibiae 222, 220 or fewer, metatarsi 222 or 221. Calamistrum subcentral to proximal, about 0.2 times length of metatarsus. Plumose hairs numerous. Trichobothria in single row on metatarsi and tarsi, 2 rows on tibiae; bothria collariform, striate. Palpal tarsi with trichobothria. Tarsal organ a low mound distal to trichobothria, pore ovoid. Male palp with embolus arising apically; a folded, membraneous conductor characteristically separated apically from the tegulum by a gap traversed by the basal part of the embolus; a large, sickle-shaped, weakly sclerotised median apophysis placed on basal tegulum; tibia with 2-3 retroventral pointed/laminate apophyses; patella with a strong apicodorsal bristle. Epigynum with a centrally membraneous fossa, lateral teeth present. Receptacula globose and contiguous. Insemination ducts short and directed laterally around receptacula from anteromedial insertions; mesal part of ducts strongly sclerotised with a small, tubercular diverticulum at junction with less sclerotised section. Spiracle narrow, placed just anterior to cribellum. Cribellum divided, triangular, posterior margin sclerotised. Spinnerets short, ALS broad and conical, PLS slender.

Included species. *Canala magna* (Berland), *C. longipes* (Berland) and *C. poya* n.sp.

Comments. Sheet web builders in cryptic surface habitats, sometimes in caves.

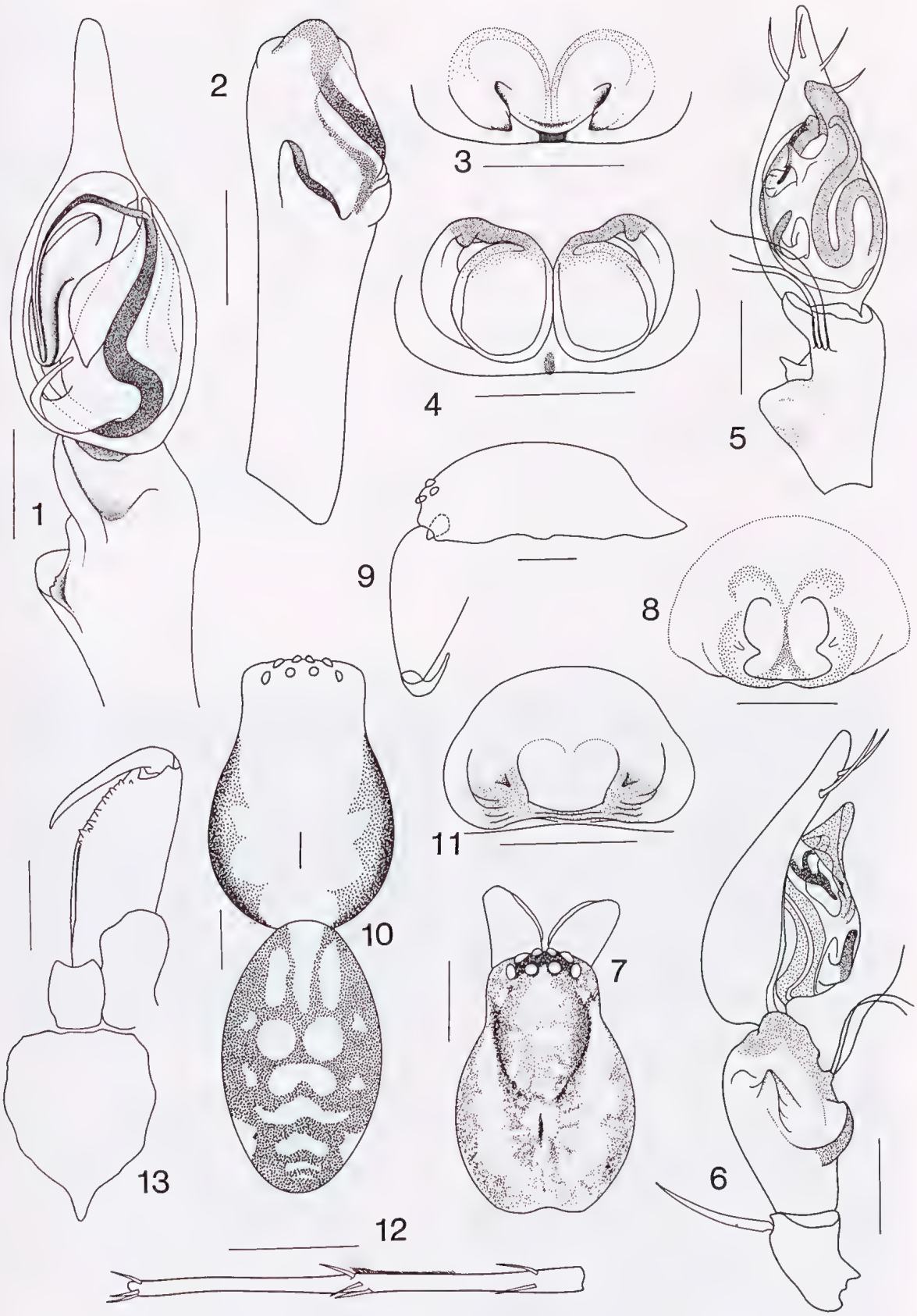
Canala magna Berland, new combination

Figs 1-4

Epimecinus magnus Berland 1924: 179, figs 26-30.
Baiami magnus.–Lehtinen 1967: 218, 331, figs 113, 117 (*Baiami magna* in caption).

Types. 5 male, 6 female COTYPES, Mont Canala, New Caledonia, Nov. 1911, AR374 (MNHN), Paris (1 male, 1 female examined).

Diagnosis. Medium sized spiders, CL male 3.60, female 5.10. Colour pattern as for genus. Chelicerae with 13-15 promarginal teeth, alternately large and small; 2 very widely spaced teeth on retromargin. Ratio eye group width to caput width 0.57:1. Foveal slit long. Ventral tibial/metatarsal spines 222/221-2. Male palp with cymbium digitiform distally; conductor folded, membraneous, retrolaterally elongate and enclosing a thin, wire-like embolus. Palpal tibia about 3.5 times longer than wide with 3 distal laminate tibial apophyses, 2 retroventral (apical and subapical), 1 retrolateral. (Note: spines, hairs abraded on male palp examined). Epigynum (Fig.3). Internal genitalia (Fig.4) with sclerotised part of insemination ducts short and narrow, running almost horizontally across anterior aspect of receptacula, diverticula directed posteriorly.



Figs 1-13. *Canala* n.gen. 1-4, *Canala magna* (Berland). 1,2, male palp: 1, ventral; 2, retrolateral tibia. 3,4, female genitalia: 3, epigynum; 4, dorsal internal. 5-8, *Canala longipes* (Berland). 5-7, male: 5, ventral palp; 6, retrolateral palp; 7, dorsal carapace. 8, female, epigynum. 9-13, *Canala poya* n.sp., female: 9, lateral carapace; 10, dorsal body; 11, epigynum; 12, dorsal metatarsus IV and calamistrum; 13, chelicera, maxilla, labium, sternum. (Scale lines: 1-4,7,11 - 0.5 mm; 5,6,8-10 - 0.25 mm; 12,13 - 1 mm)

Canala longipes (Berland) new combination

Figs 5-8

Epimecinus longipes Berland 1924: 178, figs 23-25.
Baiami magnus.–Lehtinen 1967: 218.

Types. 15 female COTYPES, AR372 (MNHN), Mont Panié, New Caledonia (1 examined).

Other material. 1 male, KS28221 (AM), Mont Panié, New Caledonia, 12 Dec. 1990, D. Bickel, 360 m.

Diagnosis. Small-medium sized spiders (CL 1.6-3). Colour pattern as for genus. Chelicerae with 7 promarginal teeth. Embolus and conductor short, apical. Male palpal tibia as long as wide with 2 apophyses (ventral laminate and retrolateral pointed). Epigynal fossa partially divided by mesally directed lobes on lateral margins on which the lateral teeth are placed (Fig.8).

Male. Measurements: CL 1.65, CW 1.18, AL 1.8, AW 1.2, EGW 0.48, MOQL 0.24, MOQAW 0.16, MOQPW 0.25, LL 0.27, LW 0.24, SL 0.89, SW 0.78. Colour pattern as for genus. Chelicerae with 7 subequal promarginal teeth; retromarginal teeth smaller, basal tooth minute. Ratio eye group width to caput width 0.66:1. Leg lengths II-IV (legs I missing), 5.40/4.88/6.63. Spination leg II: femur d113, patella d01, tibia p0110 r0010 v111(p), metatarsus p0102 r011 v022. Patellae with a small apicodorsal spine. Tibiae III,IV with 2 apical ventral spines. Male palp with cymbium conical distally; embolus short, rod-like, lying on a small, fan-shaped, membraneous conductor; tibia short, about as long as wide, with a small pointed retrolateral apophysis and a large ventral laminate apophysis; a row of 3-5 long hairs on proventral distal tibia. Patella with a strong apicodorsal and a weaker basodorsal bristle.

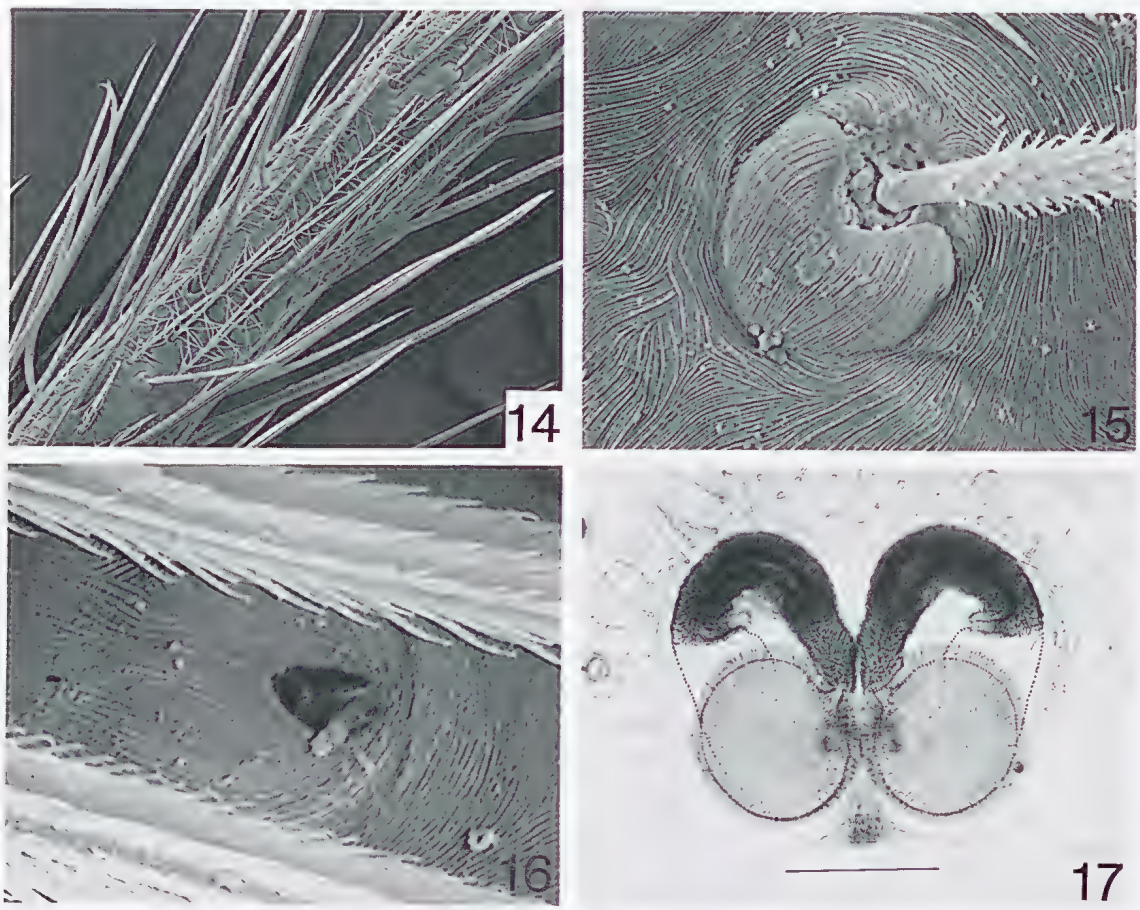
Canala poya **n.sp.**

Figs 9-17

Types. HOLOTYPE, female, BS1342 (SAM), Grotte de Ninrin-Reu, Poya, New Caledonia, 26 Dec. 1965, E. Hamilton-Smith. ALLOTYPE, female, KS28222 (AM), data as above, 11 Jan. 1966.

Other material. 2 juveniles, data as for holotype.

Diagnosis. Medium sized spiders. Chelicerae with



Figs 14-17. *Canala poya* n.sp. 14, plumose hairs, metatarsus. 15, trichobothrium base, metatarsus. 16, tarsal organ. 17, female genitalia, dorsal (scale line 0.25 mm).

8-9 promarginal teeth. Tibiae I-III lack apical spines, patellae without spines. Carapace weakly pigmented. Epigynum (Fig.11). Internal genitalia (Fig. 17).

Female. Measurements (holotype followed by paratype): CL 3.85(4.68), CW 2.64(3.22), AL 3.69(4.61), AW 2.16(2.85), EGW 1.13(1.28), MOQL 0.38(0.46), MOQAW 0.35(0.41), MOQPW 0.49(0.57), ML 1.45(1.76), LL 0.74(0.95), LW 0.59(0.65), SL 2.04(2.33), SW 1.54(1.81). Pigmentation reduced (only cavernicolous individuals seen), especially on carapace, abdominal pattern as for genus. Cheliceral promargin with 7-8 teeth, most subequal, basal retromarginal tooth very small. Ratio eye group width to caput width 0.67:1. Leg lengths I-IV, 21.21/16.71/14.17/19.26. Spination legs I,II: I, femur p010 d112/123, tibia p0110 r0110/0000 v220/020, metatarsus p0102 r0001 v221; II, d1213/113, tibia p0110 r0110 v220/120, metatarsus p1102 r0101 v221. Patellae with apicodorsal bristle. Tibiae I-III lack apical spines. Epigynum (Fig.11). Internal genitalia with sclerotised part of insemination ducts broad and strongly arched anterior to receptacula, diverticula directed medially.

Colcarteria n.gen.

Type species. *Colcarteria carrai* n.sp.

Etymology. This genus is named for the late Colin Carter, past-president of the Kempsey Speleological Society.

Diagnosis. Small cribellate spiders. Caput prominent. Cheliceral groove short with 2-4 approximated retromarginal teeth. Male palp with a large, sickle-shaped median apophysis, T-shaped conductor, tibia short with 2-3 laminate/pointed apophyses, patella with strong dorsal bristle. Epigynum with lateral teeth. Receptacula separated, ducts directed medially.

Description. Small cribellate spiders (CL 1.4-2.1). Carapace tan with grey-brown lateral caput and strial markings and marginal thoracic bands (often indistinct in cavernicolous populations). Abdomen brownish-grey with a pattern of paler chevrons. Carapace strongly arched with prominent caput. Fovea a broad slit. From above AER recurved, PER recurved-straight; From in front AER straight, PER procurved. AME smallest. Chelicerae with boss. Cheliceral groove short with 6-7 promarginal teeth in basal half of groove (4-5 small teeth plus 2 larger basal teeth) and 2-4 subequal teeth on retromargin, not widely separated. Labium about as wide as long, notched basolaterally and apically. Sternum cordate, broadly pointed posteriorly and projecting between coxae IV. Legs usually 1423, leg I 3-4 times length carapace. Trochanters notched. Legs I,II ventral spines - tibiae 122 or fewer, metatarsi 122. Calamistrum subcentral-proximal, about 0.3 times length of metatarsus. Plumose hairs numerous. Trichobothria in single row on tarsi and metatarsi, 2 rows on tibiae, bothria collariform, striate. Palpal tarsi with trichobothria. Tarsal organ a low mound distal to trichobothria, pore ovoid. Male palp with conical distal cymbium; a thin wire-like embolus; a t-shaped, membraneous conductor; a large, sickle-shaped, weakly sclerotised median apophysis, arising basally. Tibia short, about as long as wide, with a large ventral lamina and 1-2 retrolateral apophyses; a row of bristle-like hairs on distal proventral tibia. Epigynum with a centrally membraneous fossa and anterior lateral teeth; insemination ducts visible between receptacula. Receptacula globose and separated. Insemination ducts, each with a small, somewhat indistinct tubercular diverticulum, run medially between receptacula. Fertilisation ducts large. Spiracle narrow, placed anterior to cribellum, with 4 simple (undivided) tracheal tubes confined to abdomen. Cribellum with 2 narrow, well-separated fields. Spinnerets, 6, short; ALS broad, PLS longer, narrower. ALS, 2 major ampullate, 11 pyriform spigots. PMS, 1 minor ampullate, 1 cylindrical, 9-10 aciniform spigots; paracribellar spigots very few (? 2, obscured by dirt). PLS, 1 cylindrical, about 20 aciniform spigots (no paracribellar spigots seen on PMS).

Included species. *Colcarteria carrai* n.sp., *C. yessabah* n.sp., *C. kempseyi* n.sp.

Comments. These spiders build small, ground-level sheet webs with two to three entrances in moist forest habitats, notably rotting logs, and in caves. In caves webs occur in twilight and dark regions built among rocks and guano/debris on the cave floor.

The marked specific difference in retrolateral cheliceral tooth numbers (2 or 4) within this genus is unusual. The 4-tooth state is probably plesiomorphic, the loss of the two smaller apical teeth giving rise to the 2-tooth apomorphic state.

Colcarteria carrai n.sp.

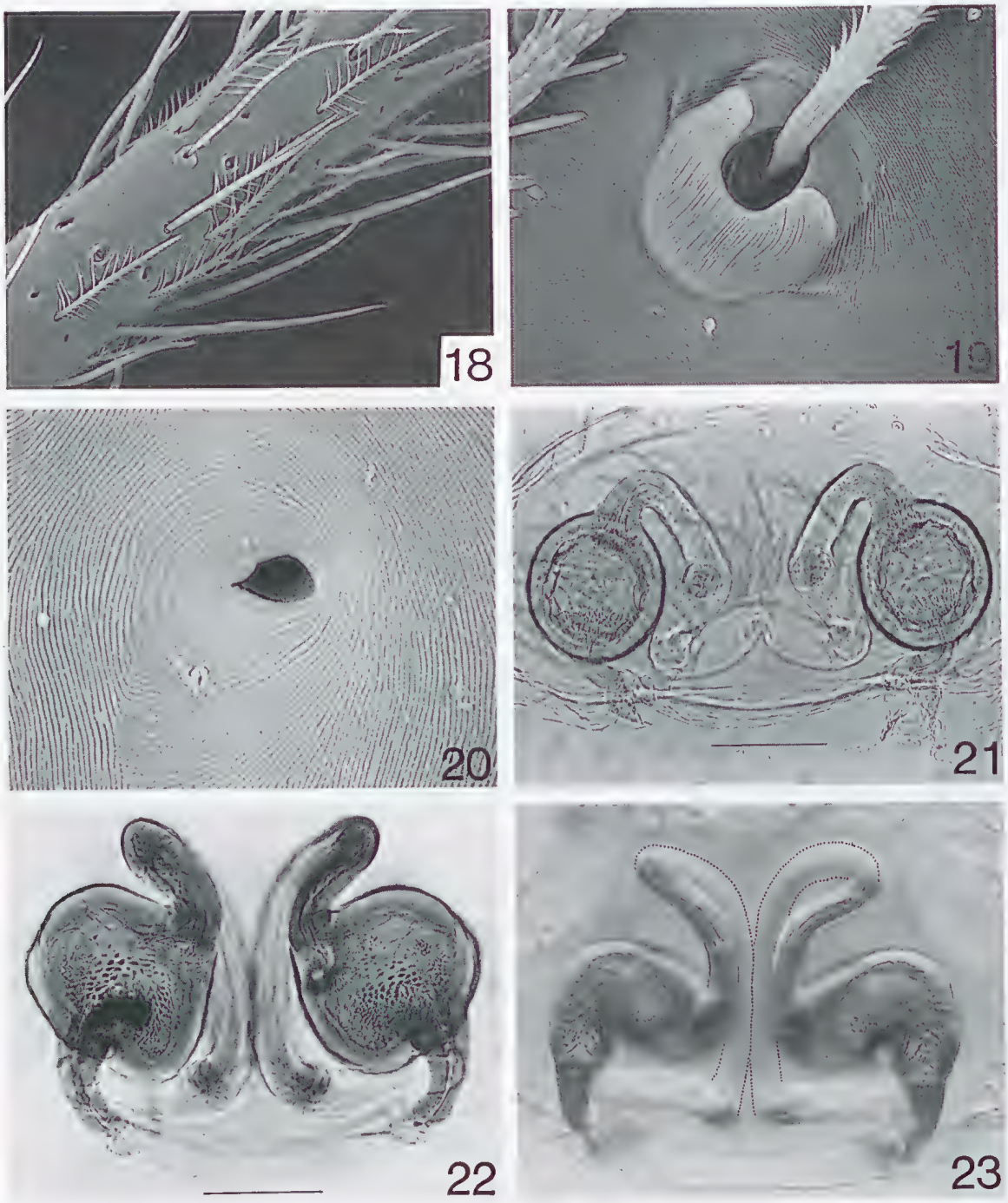
Figs 18-21, 24-34

Types. HOLOTYPE, male, KS28223 (AM), Carrai Bat Cave (SC-5), Carrai State Forest, 31°01'S 152°20'E, west of Kempsey, NSW, 25 Apr. 1974, M. Gray. ALLOTYPE, female, KS28224 (AM), data as for holotype. PARATYPES, KS28225 (AM), 9 females, 1 male, data as for holotype. KS28226 (AM), 2 males, 2 females (one used for tracheal prep. KS28227), Carrai State Forest, near Carrai Bat Cave, NSW, 26 Apr. 1974, M. Gray, in closed and tall open forest along trail to Carrai Bat Cave.

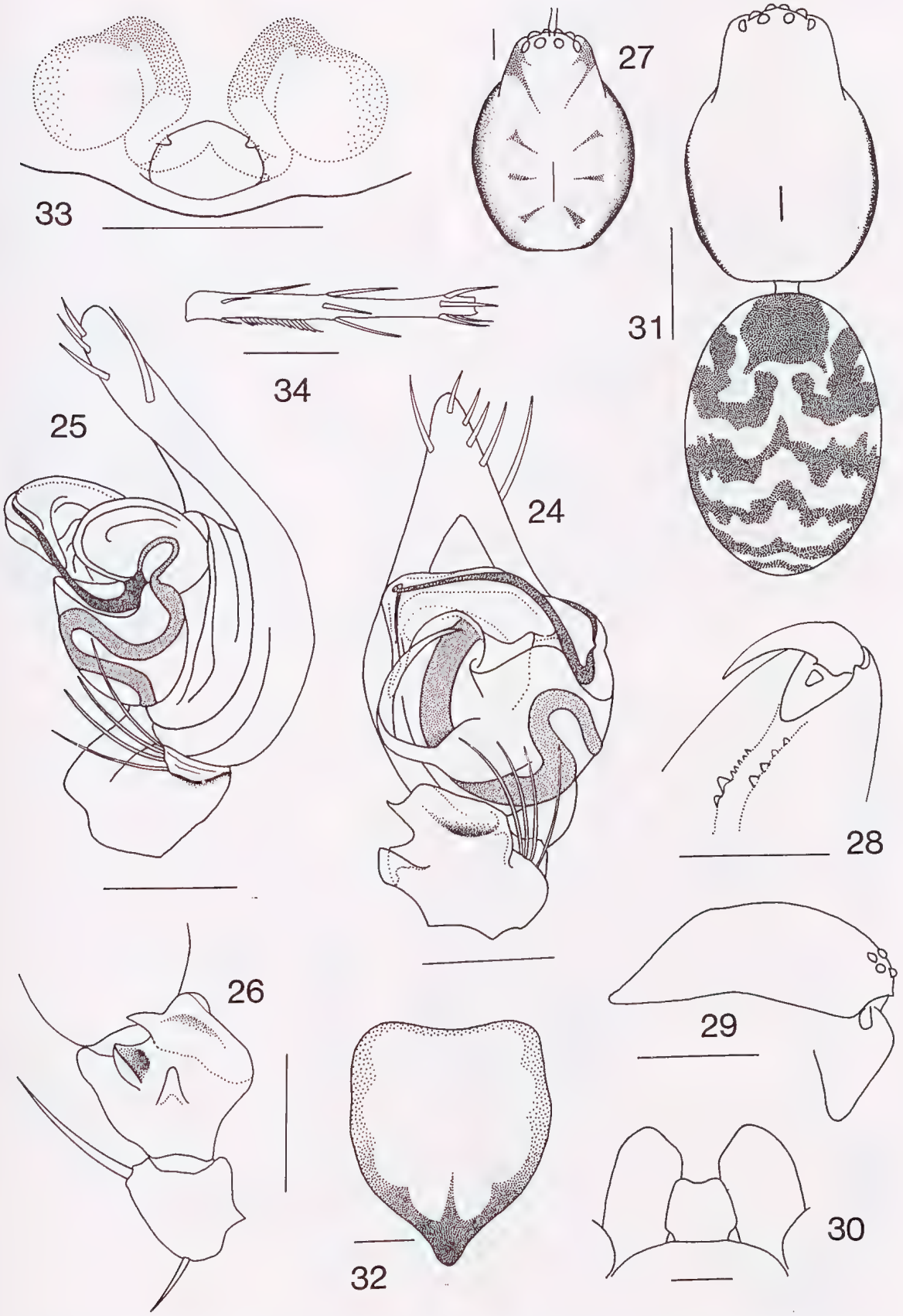
Diagnosis. Small-medium sized spiders. 3-4 teeth on cheliceral retromargin (2 in other species). Conductor wider than long. Embolus origin prolateral, subapical. Male palpal tibia with a ventral lamina and

2 retrolateral apophyses. Receptacula widely separated.

Male. Measurements: CL 1.43 (1.43-1.71), CW 1.13 (1.07-1.29), AL 1.5 (1.3-1.5), AW 1.0 (0.9-1.2), EGW 0.41 (0.38-0.47), MOQL 0.18 (0.17-0.19), MOQAW 0.16 (0.13-0.16), MOQPW 0.22 (0.18-0.24), LL 0.16 (0.16-0.22), LW 0.21 (0.20-0.26), SL 0.78 (0.77-0.92), SW 0.71 (0.63-0.71). Carapace pigmentation variable, as for genus or reduced in some cave dwelling individuals (see female Fig.31). Abdomen dorsum grey anteriorly with 6-7 narrow chevrons posteriorly. Venter with central grey stripe broken by paler patches. Cheliceral promargin with 2 basal teeth followed by 4-5 smaller teeth; 3-4 teeth on retromargin, usually smaller apically. Ratio eye width to caput width 0.73:1. Legs I,IV longest and subequal (5.70/5.68), legs II,III subequal (4.59/4.49). Spination legs I,II: I, femur d111(p)3, tibia p1010 v122/022, metatarsus p001 r001 v121; II, femur d113, tibia p1010 r0010 v122, metatarsus p1202 r102 v122. Patellae I,II,IV with short, spine-like basal and apical dorsal bristles, patella III with stronger apical spine. Embolus arises subapically, midway along prolateral tegulum; conductor wider than long. Ventral tibial apophysis pointed retrolaterally, 2 retrolateral apophyses present.



Figs 18-23. *Colcarteria* n.gen. 18-20, *C. carrai* n.sp.: 18, plumose hairs, metatarsus; 19, trichobothrium base, metatarsus; 20, tarsal organ. 21-23, female genitalia, dorsal: 21, *C. carrai* n.sp.; 22, *C. yessabah* n.sp.; 23, *C. kempseyi* n.sp. (Scale lines: 21-23 - 0.1 mm)



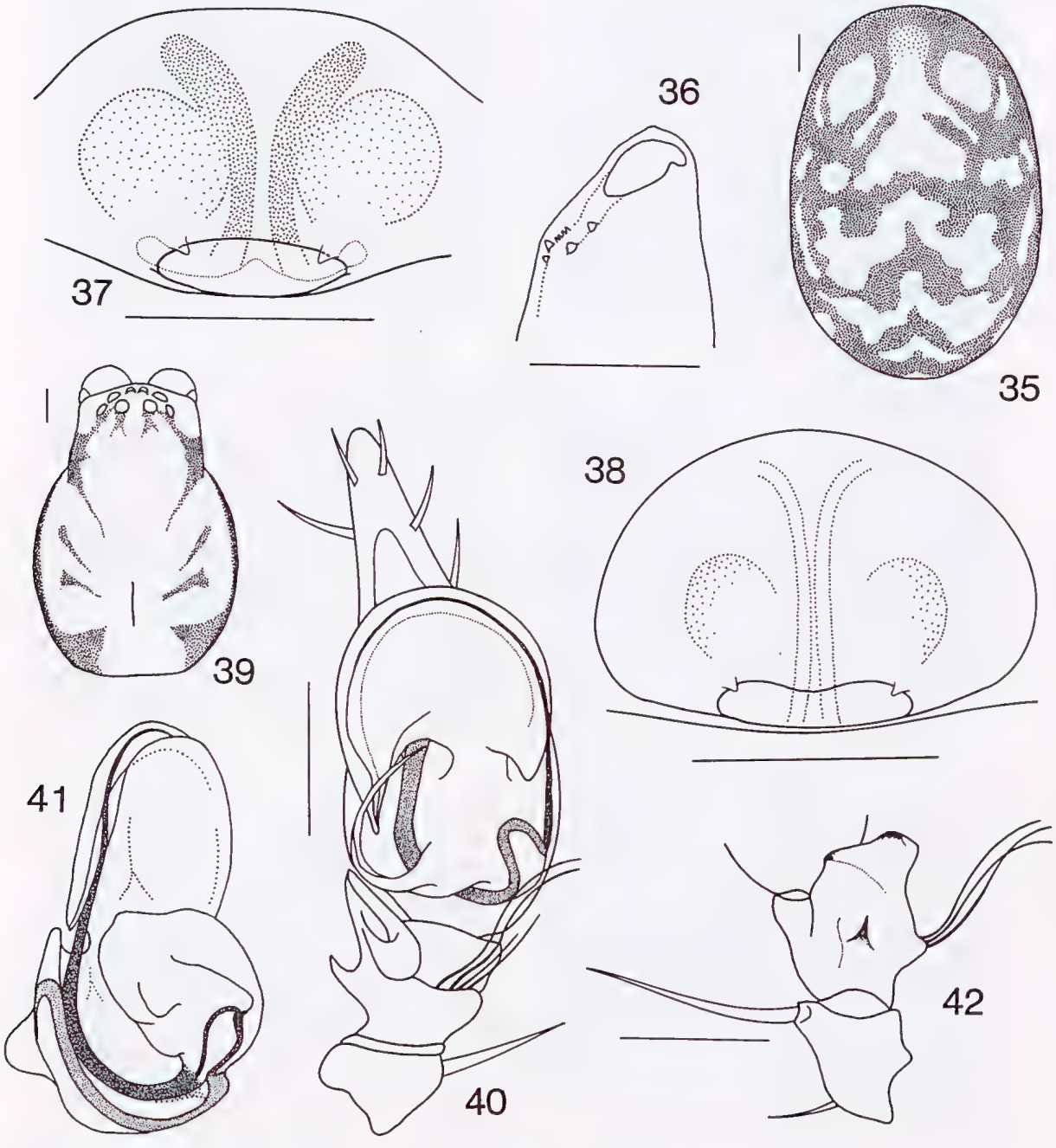
Figs 24-34. *Colcarteria carrai* n.sp. 24-26, male palp: 24, ventral; 25, prolateral; 26, retrolateral patella, tibia. 27, male carapace. 28-34, female: 28, cheliceral teeth; 29, lateral carapace; 30, maxilla and labium; 31, dorsal body; 32, sternum; 33, epigynum; 34, dorsal metatarsus IV and calamistrum. (Scale lines: 24-28,30,32,33 - 0.25 mm; 29,31 - 1 mm; 34 - 2 mm)

Female. Similar to male. Measurements: CL 1.98(1.73-2.10), CW 1.39(1.26-1.48), AL 2.3(2.0-2.6), AW 1.7(1.5-2.1), EGW 0.54(0.50-0.62), MOQL 0.24(0.19-0.24, MOQAW 0.18(0.18-0.20), MOQPW 0.28(0.25-0.30), ML 0.53(0.48-0.58), LL 0.26(0.23-0.29), LW 0.30(0.26-0.31), SL 1.07(0.95-1.10), SW 0.85(0.79-0.91). Cheliceral retromargin teeth subequal. Ratio eye group width to caput width 0.65:1. Leg lengths I-IV, 6.25/5.10/4.98/6.20. Spination legs I,II: I, femur d111(p)2, tibia v121/021(p)/020, metatarsus p001 r001 v122/121; II, femur d113, tibia p101 v122, metatarsus p102 r011 v122. Patellae as in male. Epigynum (Fig.33). Receptacula smoothly spherical-ovoid, separated by at least a diameter; insemination ducts short, separated medially, small diverticula placed at midlevel between receptacula.

Colcarteria yessabah n.sp.

Figs 22, 35-37

Types. HOLOTYPE, female, KS28228 (AM), Yessabah Bat Cave (YE-1), 31°05'S 152°43'E, near Kempsey, NSW, 18 July 1971, M. Gray. PARATYPE, females (all AM): KS28229, 2 females, data as for holotype; KS29419, 3 females, data as above, 21 July 1990, M. Gibian, entrance chamber and bat chamber passage;



Figs 35-42. 35-37, *Colcarteria yessabah* n.sp., female: 35, dorsal abdomen; 36, cheliceral teeth; 37, epigynum; 38-42, *Colcarteria kempseyi* n.sp. 38,39, female: 38, epigynum; 39, carapace. 40-42, male palp: 40, ventral; 41, prolateral, bulb only; 42, retrolateral patella and tibia. (Scale lines: 0.25 mm)

KS29420, 1 female, data as above, 29 Sept. 1990, entrance chamber.

Diagnosis. Small-medium sized spiders. Cheliceral retromargin with 2 teeth. Receptacula not widely separated. Insemination ducts converge between receptacula, longer than in *C. carrai* but shorter and broader than in *C. kempseyi*.

Female. Measurements: (paratype KS28229 in parentheses) CL 2.04(2.10), CW 1.48(1.51), AL 2.5(2.6), AW 1.8(1.8), PERW 0.55(0.56), MOQL 0.25(0.24), MOQAW 0.19(0.20), MOQPW 0.28(0.29), ML 0.58(0.59), LL 0.30(0.28), LW 0.34(0.31), SL 1.13(1.14), SW 0.93(0.93). Colouration similar to *C. carrai*. Abdomen with pale, irregular mid-dorsal stripe anteriorly, pale suffusion often laterally diffused. Cheliceral promargin teeth like *C. carrai*, retromargin with 2 teeth. Ratio eye group width to caput width 0.65:1. Leg lengths I-IV, 7.82/6.04/5.35/7.41. Spination legs I,II: I, femur d111(p)/111(p)1(p), patella d0(1), tibia v020, metatarsus v222; II, femur d113, patella d0(1), tibia p110 d(1)0 v222, metatarsus p001 r001 v222. Epigynum (Fig.37). Receptacula large, irregularly rounded, separated by less than a diameter. Insemination ducts arise anteromedially from receptacula and diverge across their anteromedial surfaces before converging (contiguous or subcontiguous) between them; the small diverticula are placed posteriorly between receptacula.

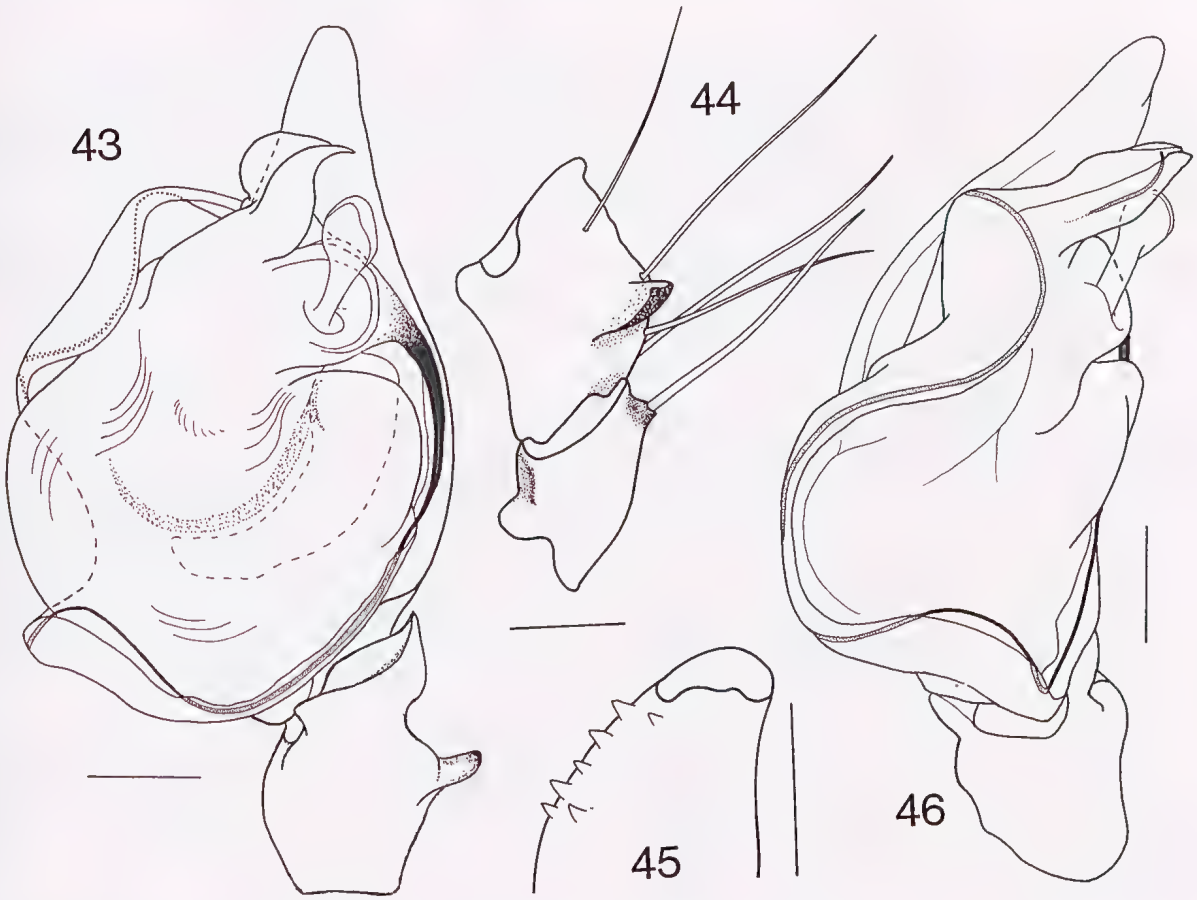
Colcarteria kempseyi n.sp.

Figs 23, 38-42

Types. HOLOTYPE, male, KS28230 (AM), Maria River State Forest, 31°11'S 152°50'E, near Kempsey, NSW, 23 Apr. 1974, M. Gray; tall open forest (*Eucalyptus gummifera*). ALLOTYPE, female, KS28231 (AM), data as for holotype.

Diagnosis. Small spiders. Cheliceral retromargin with 2 teeth. Insemination ducts thin, elongate, converge medially anterior to receptacula. Conductor large, semicircular. Embolus origin basal. Male palpal tibia with a ventral lamina and 1 retrolateral apophysis.

Male. Measurements: CL 1.50, CW 1.06, AL 1.5, AW 0.9, EGW 0.38, MOQL 0.18, MOQAW 0.15, MOQPW 0.18, LL 0.18, LW 0.22, SL 0.82, SW 0.66. Ratio eye group width to caput width 0.72:1. Moderately pigmented, pattern as for genus, abdomen similar to *C. yessabah*. Cheliceral teeth as for *C. yessabah*. Leg lengths I-IV, 5.59/4.29/3.92/5.29. Spination legs I,II: I,



Figs 43-46. *Forsterina koghiana* n.sp., male. 43-45, palp: 43, ventral; 44, retrolateral patella and tibia; 45, prolateral. 46, cheliceral teeth. (Scale lines: 43-45 - 0.25 mm; 46 - 0.5 mm)

femur d111(p)3, patella d01, tibia p110 v222, metatarsus p001 v222; II, femur d113, patella d01, tibia d(1)010 p110 r010 v222, metatarsus p111 r001, v222. v221. Patellae dorsal spines largest on legs III,IV. Male palp with large semicircular conductor, about as long as wide. Embolus origin on basal prolateral tegulum. Ventral tibial apophysis bluntly pointed retrolaterally; 1 retrolateral apophysis.

Female. Measurements: CL 1.73, CW 1.28, AL 1.7, AW 1.8, EGW 1.95, MOQL 0.20, MOQAW 0.19, MOQPW 0.26, ML 0.53, LL 0.25, LW 0.28, SL 0.96, SW 0.78. Ratio eye group width to caput width 0.71:1. Leg lengths I-IV, 6.36/4.94/4.55/6.16. Spination legs I,II: I, femur d111(p)0, patella d01, tibia v1(p)20, metatarsus p001 r001 v221; II, femur d113, patella d01, tibia d(1)00 p110 v01(r)1(p), metatarsus p012 r011 v221. Epigynum with thin, longitudinal insemination ducts visible medially. Receptacula gourd-shaped, separated by less than a diameter. Insemination ducts similar to *C. yessabah* but more elongate and slender, arising medially from receptacula, curving well above them to become contiguous anteriorly.

Comments. Female internal genitalic and cheliceral tooth structure suggests that *C. kempseyi* and *C. yessabah* are more closely related than either is to *C. carrai*.

Forsterina koghiana n.sp.

Figs 43-46

Type. HOLOTYPE, male, KS28232 (AM), Mont Koghi, near Noumea, New Caledonia, 8 July, 1963.

Diagnosis. Male palp with loosely sinuous conductor and embolus. Median apophysis narrow basally. Retrolateral apophysis placed midway along tibia (basal in *F. alticola* (Berland)).

Male. Measurements: CL 2.99, CW 1.95, (abdomen damaged), ERW 0.87, MOQL 0.40, MOQAW 0.34, MOQPW 0.44, ML 0.93, LL 0.48, LW 0.44, SL 1.62, SW 1.25. Chelicerae with 5-6 promarginal teeth (including 1 or 2 small teeth anterior to second basal tooth) and 2 well separated retromarginal teeth; a row of about 17 short hairs behind basal prolateral teeth. Leg lengths I-IV, 12.29/10.16/8.97/10.84. Spination legs I,II: I, femur d12(r small)1(p)3, tibia p1110 r1010 v222, metatarsus p011 r011 v222; II, femur d12(r small)3 or 133, tibia p0101 r1010 v222, metatarsus p111 r0101 v222. Male palp with conductor and embolus loosely overlapping tegulum basally and proapically. Embolus arises apically, retrolateral to median apophysis. Median apophysis with narrow, stalk-like base. Retrolateral tibial apophysis placed midway along tibia.

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New Species of the Trapdoor Spider Genus *Misgolas* Karsch (Mygalomorphae: Idiopidae) with a Review of the Tube-building Species

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ABSTRACT. Four sympatric species of *Misgolas* Karsch are studied: *M. hubbardi* n.sp., *M. dereki* n.sp., *M. kirstiae* n.sp., and *M. robertsi* (Main & Mascord, 1974). The male paratype of the tube building spider *M. robertsi* (originally *Dyarcyops robertsi*) from Dorrigo, NSW is removed from that species and designated as the holotype of *Misgolas mascordi* n.sp. The species *M. robertsi* is reconsidered and its male is identified and described. Biological notes are included.

WISHART, G., 1992. New species of the trapdoor spider genus *Misgolas* Karsch (Mygalomorphae: Idiopidae) with a review of the tube-building species. Records of the Australian Museum 44(3): 263–278.

From field studies and examination of specimens held by the Australian Museum it appears that the idiopid trap-door spider genus *Misgolas* Karsch, 1878 may be represented in the Sydney-Illawarra region by at least seventeen species of which only six have been described: *M. rapax* Karsch, 1878, *M. biroi* (Kulczynski, 1908), *M. elegans* (Rainbow & Pulleine, 1918), *M. gracilis* (Rainbow & Pulleine, 1918), *M. maculosus* (Rainbow & Pulleine, 1918) and *M. robertsi* (Main & Mascord, 1974). Apart from *M. rapax*, the type species of *Misgolas*, the other species were originally described in either the genera *Arbanitis* Koch or *Dyarcyops* Hogg (Main, 1985a,b). Only *M. robertsi* has a male description the remaining species' descriptions being based on less reliable female characters such as eye pattern and dorsal abdominal pattern.

Specimens held in the Australian Museum and attributed to *M. rapax* by Main (1985a,b) were examined, together with specimens of *M. elegans* (Rainbow & Pulleine, 1918). From morphological differences between these specimens and those collected from the remnant forest at "Scalloway", Gerringong (34°44'11"S, 150°47'23"E), it is concluded that the Gerringong specimens represent four sympatric distinct species, three of which are newly described in this paper and the one remaining is the tube building spider *M. robertsi* (Table 1 [see Appendix]).

Main & Mascord (1974) suggested that although disjunct populations of tube-building species of *Misgolas* might be one or several species, it was most appropriate to consider them to represent the one species, *Dyarcyops robertsi* Main & Mascord, 1974. A female from southern NSW was described as the holotype and a male from northern NSW as a paratype. In this paper I show that subsequent examination of males from both northern and southern locations, confirm that there are at least two species in this tube-building group.

Materials and Methods

Measuring points for morphological features are taken from Coyle (1971) with the addition of the post foveal height which is the height of the thorax taken from the highest point posterior to the fovea viewed laterally. The caput ratio is the ratio of the caput height to the post foveal height where the post foveal height is taken as unity and is an indication of the relative height of the caput. Linear measurements are expressed in millimetres. The Tibial Index is taken from Petrunkevitch (1942) and is that used by Main (1985a). Measurements and counts refer to the characters on the right side of the specimen with data for the left side given in brackets. Notation of spines is taken from Forster & Wilton (1968).

Male palpal organ variation was found to be consistent within species in *Misgolas*. Whilst at rest the bulb is folded into the ventral cavity of the palpal tibia. Usually the brown sclerotised convex side is uppermost against the tibia cavity and it is considered here to be the dorsal surface. The weakly chitinised flange is retrolaterally situated on the basal part of the embolus. In females the most useful character for species identification and male-female association is differences in the abdominal ventral pattern.

Abbreviations used throughout the text are: d – dorsal; v – ventral; p – prolateral; pd – prodorsal; pv – proventral; r – retrolateral; rd – retrodorsal; rv – retroventral; ALE – anterior lateral eyes; AME – anterior median eyes; PLE – posterior lateral eyes; PME – posterior median eyes; PMS – posterior median spinnerets; AM – Australian Museum, Sydney; GW – collected by G. Wishart.

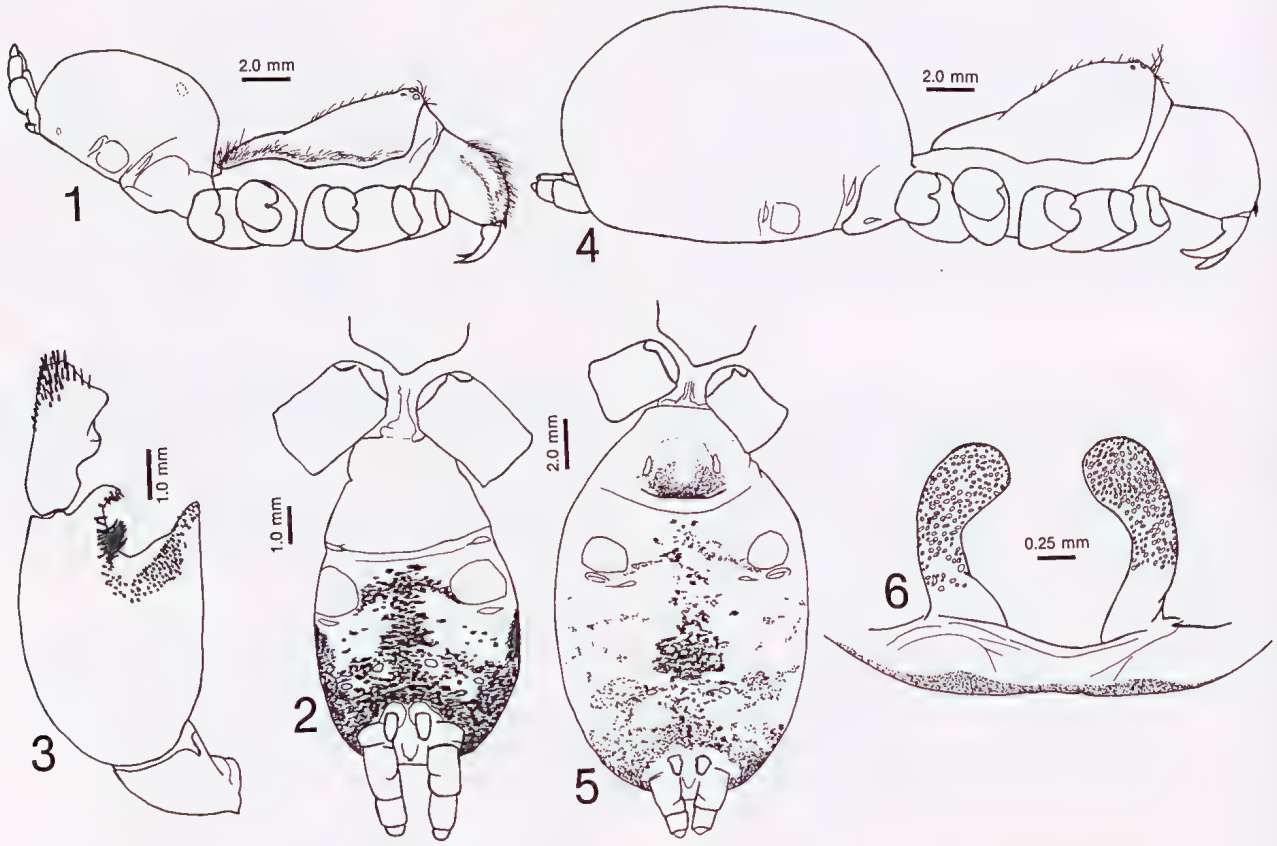
Misgolas hubbardi n.sp.

Figs 1-6, 28,29

Material examined. HOLOTYPE, male, KS22301(AM). "Scalloway", Willowvale, near Gerringong, NSW (34°44'11"S 150°47'23"E), 17 Dec. 1985, GW.

ALLOTYPE, female, KS22302(AM). Locality as above, 10 June 1985, GW.

PARATYPES (all AM; excepting where otherwise specified locality as above). *Males:* KS22303, 7 Apr. 1985, GW; KS22304, 29 Dec. 1985, GW; KS22305, 18 Apr. 1987, GW; KS22306, 8 Dec. 1986, GW; KS22307, 11 Dec. 1986, GW; KS22308, 25 Jan. 1987, GW; KS22309, 30 May 1988, GW (mated with KS22319 on 5 June 1988); KS22310, 22 May 1987, GW; KS22311, Jupiter Street, Gerringong (34°45'2"S 150°49'31"E), 20 Dec. 1978, K. Vaux; KS22312, Rowlins Road, Gerringong (34°44'45"S 150°49'12"E), 15 Aug. 1981, K. Davidson; KS22313, Greta Street, Gerringong (34°44'54"S 150°49'24"E), 3 Mar. 1984, S. Hall; KS22314, Belinda Street, Gerringong, (34°44'57"S 150°49'34"E), 7 Aug. 1984, R.Waite; KS22315, Jupiter Street, Gerringong (34°45'6"S 150°49'46"E), 24 Dec. 1986, R. Feeney; KS22316,



Figs 1-6. *Misgolas hubbardi* n.sp.: 1-3, male holotype. 1, body lateral; 2, abdomen ventral; 3, right palpal tibia and cymbium retrolateral. 4-5, female allotype. 4, body lateral; 5, abdomen ventral. 6, female paratype KS22317 internal genitalia dorsal.

19 June 1987, GW.

Females: KS22317, 2 Aug. 1987, GW (genitalia dissected); KS22318, 27 Sept. 1986, GW; KS22319, 9 Aug. 1987, GW, (mated with KS22309 on 5 June 1988); KS22320, 2 Aug. 1988, GW; KS22321, 7 Mar. 1987, GW; KS22322, 26 Mar. 1987, GW; KS22323, Mayflower Village, Gerringong (34°44'54"S 150°49'13"E), 19 Apr. 1989, GW; KS22324, 29 Nov. 1986, GW; KS22325, 16 Nov. 1986, GW.

Diagnosis. Large brown spiders; retrodorsal surface of metatarsi IV without spines. In female, carapace length 10.0-13.7; fovea strongly procurved; abdomen with indistinct dorsal pattern, venter pattern as figured (Fig.5). In male, carapace length 8.2-10.5; all tarsi without spines; embolus of bulb with retrolateral flange with about five folds; embolus apically twisted clockwise through 90° and armed prolaterally with a subdistal thorn-like apophysis (Figs 28-29). Cymbium with peglike spines on distal third of dorsal surface.

Male holotype (Figs 1-3, 28,29). *Size.* Carapace length 9.31, width 7.81, height 3.25, post foveal height 1.69. Caput ratio 1.92. Abdomen length 8.73, width 5.66.

Colour. Carapace dark tan, in life bedecked with golden hirsute sheen. Legs paler distally; lateral surfaces of palps and legs I and II with some conspicuous longitudinal dark brown smudges. Abdomen dark brown dorsally with indistinct pattern of yellow bands in bilateral series of seven. Venter pale yellow with dark brown speckle becoming more dense maculation and broadening adjacent to spinnerets.

Carapace. Edge fringed with black bristles which encroach onto posterior third of post foveal surface. Posterior edge slightly recurved, almost truncate. Striae glabrous. Line of 12 median bristles occupies low caput arch. Fine golden hairs and band of small bristles prolaterally adjacent to each anterior stria. Group of 4 anteriorly inclined bristles between PME; group of six posteriorly inclined bristles in front of AME. Fovea width 1.30, slightly procurved, glabrous.

Eyes. Placed on low tubercle; anterior width 1.56, posterior width 1.33, length 0.86. Line joining the posterior edges of ALE transects the anterior quarter of AME. Posterior row slightly procurved in front, recurved behind.

Chelicerae. Rastellum with first row of 6(5) short strong spines and second row of 7(5) smaller spines. Small pallid intercheliceral tumescence has covering of fine setae. Fang groove with 8(9) promarginal teeth, and 15(12) small retromarginal/intermediate row teeth beginning adjacent to fourth distal promarginal tooth and terminating slightly beyond proximal promarginal tooth.

Labium. Length 0.97, width 1.37, separated from sternum by broad continuous suture.

Maxillae. About 50(48) anteroental pointed cuspules with constricted base, few surmounted by fine hair.

Sternum. Length 4.91, width 3.86. Anterior sigilla small, round, submarginal; middle and posterior sigilla progressively larger, ovate and distant from margin.

Legs. Limb measurements: leg formula – 4 1 2 3. Width of patella I, 1.68; tibial index leg I, 17.20. Width of patella IV, 1.60; tibial index leg IV, 14.75.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Palp	5.00	2.44	5.00	–	2.74	15.18
I	7.91	3.94	5.83	6.71	4.10	28.49
II	7.22	3.63	5.19	5.73	3.71	25.48
III	5.89	2.98	3.78	5.09	3.33	21.07
IV	8.30	3.71	7.14	7.14	3.94	30.23

Palp (Fig.3) with dense cluster of peg-shaped spines evenly distributed over distal third of dorsal surface of cymbium, progressively longer towards apex of segment. Tibia with large retroventral apophysis covered dorsally with short spines; ventral surface of tibial excavation with medially placed extended brush of long spines and hooked apical apophysis to which is attached a small terminal tuft of short spines. Bulb with retrolateral embolic flange with four or five folds; embolus twisted clock-wise through 90°; subdistal thorn shaped apophysis on embolus. Scopula dense on tarsi I and II, sparse on tarsi III and IV; incomplete and dense on metatarsi I and II and incomplete and sparse on metatarsi III and IV. Tibia I with apical bifid apophysis; distal process with 3(2) spines, proximal process with 2(3) spines.

Trichobothria. Palp: tarsi 10(12), tibia pd6(6) rd7(7). Leg I: tarsi 13(14), metatarsi 16(14), tibia pd8(8) rd6(6). Leg II: tarsi 14(13), metatarsi 15(13), tibia pd7(8) rd7(7). Leg III: tarsi 12(11), metatarsi 13(13), tibia pd8(6) rd7(7). Leg IV: tarsi 12(13), metatarsi 17(15), tibia pd7(7) rd8(8).

Leg spination. Spines absent from all tarsi. Leg I: metatarsi v0100(011000); tibia v01111102(01110002) pd010(000). Leg II: metatarsi v0202(0100); tibia v0211112(011112), pd001010(001010), p01(01). Leg III: metatarsi v0102013(0002002), d002120(002020); tibia v0123(0123), p0110(0110), r001010(001010); patella pd5(3) including 1(0) on distal edge. Leg IV: metatarsi v0110212(01001101); tibia v01101102(01101102); femur about pd26(26) distal spines.

Abdomen. Dorsum covered with long fine dark bristles, hairs only on ventral surface.

Female allotype (Figs 4-6). *Size.* Carapace length 10.49, width 8.43, height 4.61, post foveal height 1.76. Caput ratio 2.62. Abdomen length 17.18, width 11.66.

Colour. Abdomen pale yellow, ventrally some dark brown speckles forming a short dark median band which widens into a broad maculated pattern in front of spinnerets.

Carapace. Posterior edge broadly recurved. Edge fringed with long fine light hairs which encroach onto posterior two thirds of post foveal surface. Striae glabrous and well defined. Line of eight median bristles along caput arch. Group of 5 anteriorly inclined bristles between PME; group of 4 posteriorly inclined bristles in front of AME. Fovea width 1.86, procurved, glabrous.

Eyes. AME placed on a low mound; anterior width 1.83, posterior width 1.75, length 1.08. Line joining posterior edges of ALE and anterior edges of AME is

straight. Posterior row procurved in front, recurved behind.

Chelicerae. Rastellum with first row of 8(7) strong blunt spines, second row of 11(9), disordered third row and a few smaller spines retreating along the prodorsal cheliceral edge. Fang groove with 9(8) promarginal teeth and 18(19) smaller retromarginal/ intermediate row of teeth beginning adjacent to third distal promarginal tooth and extending 4(4) teeth beyond proximal promarginal tooth.

Labium. Length 1.42, width 1.99, separated from sternum by deep continuous suture.

Maxillae. About 54 (55) anteroental fusiform cuspules.

Sternum. Length 5.68, width 4.87.

Legs. Limb measurements: leg formula – 4 1 2 3. Width of patella II, 1.83; tibial index leg I, 18.77. Width of patella IV, 2.04; tibial index leg IV, 18.15.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Palp	6.38	3.33	3.53	–	4.27	17.51
I	7.84	4.75	5.00	4.31	2.73	24.63
II	7.19	4.31	4.16	3.84	2.58	22.08
III	5.56	3.61	2.97	3.29	2.43	17.86
IV	7.94	4.55	6.69	5.63	2.84	27.65

Dense scopula complete on tarsi of palp, legs I and II and incomplete on metatarsi of legs I and II.

Trichobothria. Palp: tarsi 12(13), tibia pd8(8) rd9(8). Leg I: tarsi 16(15), metatarsi 18(20), tibia pd9(10) rd8(8). Leg II: tarsi 16(16), metatarsi 21(15), tibia pd10(9) rd9(8). Leg III: tarsi 15(15), metatarsi 15(15), tibia pd8(8) rd8(8). Leg IV: tarsi 15(16), metatarsi 16(18), tibia pd10(10) rd9(10).

Leg spination. Palp: tarsi pv2(2) subproximal, rv01000(01000) plus about v28 subproximal long bristles; tibia pv9(9) rv5(6). Leg I: metatarsi v012002(012001); tibia v011112(021112). Leg II: metatarsi v0110003 (022000); tibia v0111111(0212103). Leg III: tarsi v15(14) in scattered group; metatarsi v03223(02213) d002120 (002120); tibia v0222(0223) p0110(01110) r001010 (001010); patella pd4(6) nil on distal edge. Leg IV: tarsi v17(19) in scattered group; metatarsi v16(16) in scattered group; patella pd10(10) proximal cluster; femur pd40(40) distal group.

Abdomen. Dorsum covered with dark hairs.

Genitalia. Sclerotised lip of epigynum strongly recurved with broad medial indentation. Spermathecae in paratype KS22318 consist of a pair of long vesicles each with a terminal swelling (Fig.6).

Etymology. The species is named in honour of the late Mr Frederick C. Hubbard who collected the first spider from "Scalloway" for taxonomic examination at the Australian Museum.

Distribution and natural history. The species is common in the Gerringong district and north to Kiama.

The burrow has a rigid, funnel-like entrance; the lip is always oblique at an angle of between 30° and 80° in the manner of a hood and is disguised and strengthened with attached leaves and other small pieces of vegetation. The female has been observed to vacate the burrow and gather vegetation fragments from up to 30 cm away. The burrow tube extends vertically downwards for about 30-40 cm. A typical tube is 35 cm long, 3.5 cm wide at the entrance and narrowing rapidly to 2 cm wide. The tube is lined with strong silk which becomes weaker and more flexible towards the base where it opens into an enlarged earthen retreat. About halfway down the tube there is a weakened band or joint behind which rejected exuviae are placed.

Mature males wander throughout each year with the greatest concentrations during April, May, June and July and during November, December and January.

Misgolas dereki n.sp.

Figs 7-12, 30,31

Material examined. HOLOTYPE, male, KS22326(AM). "Scalloway", Willowvale, near Gerringong, NSW (34°44'11"S 150°47'23"E), 17 Oct. 1985, GW.

ALLOTYPE, female, KS22327(AM). Locality as above, 13 Jan. 1986, GW.

PARATYPES (all AM; excepting where otherwise specified locality as above). Males: KS22328, 22 May 1985, GW; KS22329, 6 July 1985, GW; KS22330, 20 Apr. 1986, GW; KS22331, 11 Apr. 1986, P. Askew; KS22332, 21 May, 1986, GW; KS22333, 10 Apr. 1987, GW; KS22334, 8 May 1987, GW; KS22335, 18 May 1987, GW; KS22336, 7 Sept. 1985, GW; KS22337, Blackwood Street, Gerringong (34°44'48"S 150°49'24"E), 16 Apr. 1989, S. Mace; KS22338, Blackwood Street, Gerringong, 26 Apr. 1989, S. Mace; KS22339, "Rockfield Park" Berry (34°45'56"S 150°37'13"E), 16 June 1986, F. Swane; KS22340, Minnamurra Falls National Park (34°38'30"S 150°45'E), 23 Mar. 1988, R. Standen; KS22341, Wilson Avenue, Gerringong (34°44'38"S 150°49'38"E), 28 Apr. 1989, S. Prosser; KS22342, 16 May 1987, GW. Females: KS22343, 19 May 1985, GW (genitalia dissected, some legs damaged); KS22344, 20 May 1985, GW; KS22345, 7 Dec. 1985, GW; KS22346, 4 Jan. 1989, GW (genitalia dissected); KS22347, Kiama (34°40'S 150°51'E), 10 Jan. 1981, GW; KS22348, Far Meadow, near Berry (34°49'S 150°43'E), 5 Mar. 1989, S. Mace; KS22349, 26 Apr. 1986, GW (some damaged limbs); KS22350, 26 Apr. 1986, GW (with some spiderlings); KS22351, 27 Dec. 1985, GW; KS22352, Kiama (34°40'S 150°51'E), 12 Oct. 1986, K. Mitchell; KS22353, Kiama (34°40'19"S 150°51'0"E), 13 Jan. 1988, Rod Wishart; KS22354, Tombonda Drive, Kiama (34°41'14"S 150°51'17"E), 29 May 1988, GW.

Diagnosis. Medium sized brown spiders; dorsum of abdomen with pattern of transverse bands; venter entirely pale except for sparse scattered dark brown speckles (Figs 8,11). In female carapace length 7.7-11.5; fovea slightly procurved almost straight; spination of retrodorsal surface of metatarsi IV, 001010. In male carapace length 6.0-8.1; spines present on tarsi III and IV; embolus of male bulb with retrolateral flange with three prominent folds; a small thornlike apophysis is placed dorsally about halfway along embolus (Figs 30,31). Cymbium with sparse distal group of long spines on dorsal surface.

Male holotype (Figs 7-9,30,31). *Size.* Carapace length 7.12, width 5.75, height 2.17, post foveal height 1.53. Caput ratio 1.42. Abdomen length 7.19, width 4.28.

Colour. Carapace dark tan, in life bedecked with golden hirsute sheen. Legs paler distally; lateral surfaces of palps and legs I and II with indistinct darker smudges. Abdomen dorsum dark brown with distinct pattern of pale yellow bands in bilateral series of eight. Venter pale with some very sparse scattered dark brown speckles most concentrated behind epigastric furrow.

Carapace. Edge fringed with black bristles which encroach sparsely onto posterior half of post foveal surface. Posterior edge recurved. Striae glabrous. Line of 11 median bristles occupy length of low caput arch. Fine golden hairs and line of small bristles prolaterally adjacent to each anterior stria; hairs terminate at foveal edge. Group of 7 anteriorly inclined bristles between PME; group of 12 posteriorly inclined bristles in front of AME. Fovea width 1.21, recurved.

Eyes. Placed on low tubercle; anterior width 1.10, posterior width 0.99, length 0.86. Line joining the posterior edges of ALE transects the anterior third of AME. Posterior row straight in front, slightly recurved behind.

Chelicerae. Rastellum with first row of 5(5) short strong spines and second row of 2(2) smaller spines. Pallid intercheliceral tumescence has covering of dark setae concentrated proximally. Fang groove with 9(9) large promarginal teeth and 9(9) small retromarginal/intermediate row teeth beginning adjacent to the fifth (fourth) distal promarginal tooth and terminating slightly beyond proximal promarginal tooth.

Labium. Length 0.74, width 1.04, separated from sternum by broad continuous suture.

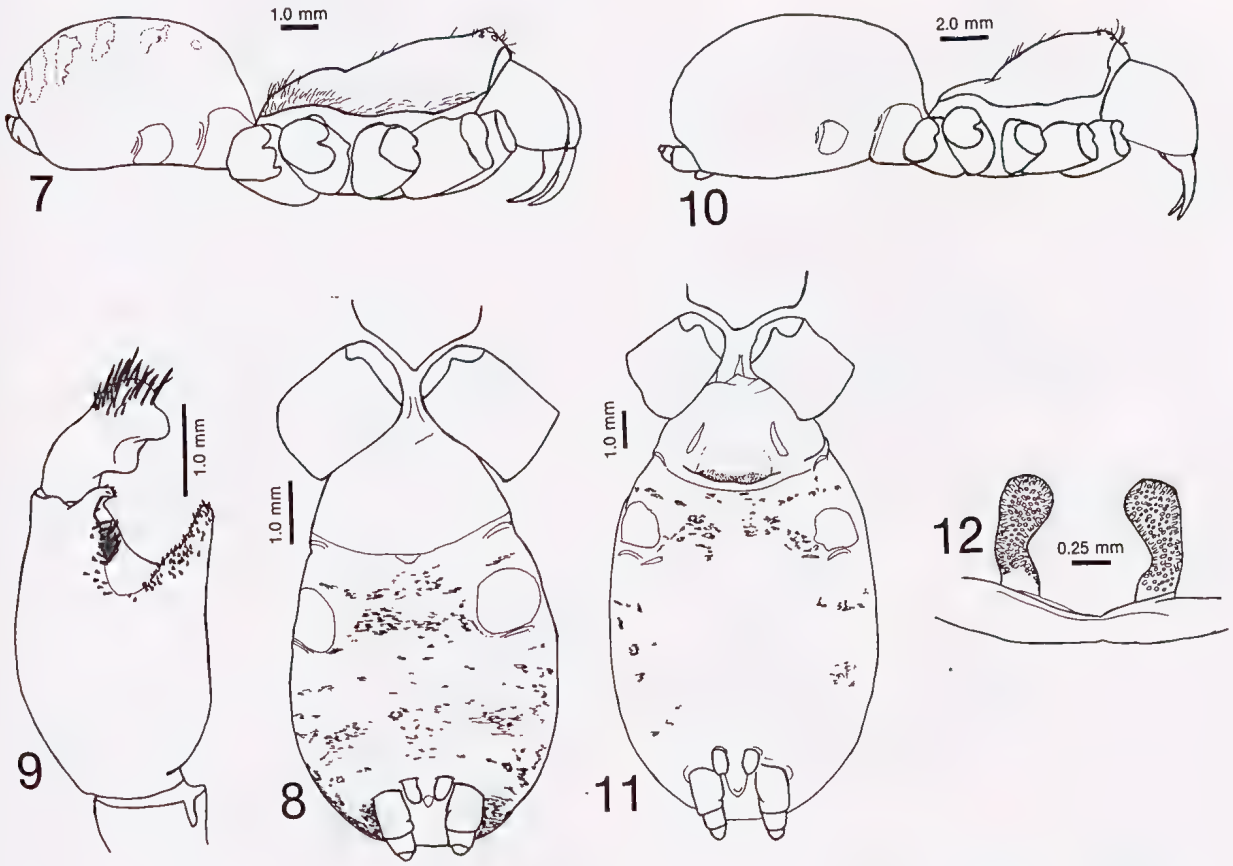
Maxillae. About 45(46) anteroental mostly blunt cuspules.

Sternum. Length 3.84, width 2.64. Anterior sigilla small, round, submarginal; middle and posterior sigilla progressively larger, ovate and distant from margin.

Legs. Limb measurements: leg formula 4 1 2 3. Width of patella I, 1.17; tibial index leg I, 15.92. Width of patella IV, 1.27; tibial index leg IV, 15.41.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Palp	3.63	1.78	3.53	–	1.70	10.64
I	6.26	3.20	4.15	4.66	2.87	21.14
II	5.70	2.95	3.88	4.19	2.69	19.41
III	4.38	2.26	2.64	3.72	2.49	15.49
IV	5.98	3.02	5.22	5.37	3.08	22.67

Palp (Fig.9) with sparse cluster of long weak spines distributed distally over dorsal surface of cymbium. Tibia with large retroventral apophysis covered dorsally with short spines; ventral surface of tibial excavation with few scattered short spines, in midregion an extended brush of about 14 long spines and a hooked apical apophysis to which is attached



Figs 7-12. *Misgolas dereki* n.sp.: 7-9, male holotype. 7, body lateral; 8, abdomen ventral; 9, right palpal tibia and cymbium retrolateral. 10-11, female allotype. 10, body lateral; 11, abdomen ventral. 12, female paratype KS22343 internal genitalia dorsal.

small terminal tuft of about 10 short spines. Bulb with retrolateral embolic flange with 3 prominent folds; embolus arched, not twisted; thornlike apophysis is dorsally placed about halfway along embolus. Scopula dense on tarsi I and II, very sparse on tarsi III and IV; incomplete and sparse on metatarsi I and II; almost absent on metatarsi III and IV and retrolateral surface of metatarsi II. Tibia I with apical bifid apophysis; distal process with 4(6) spines, proximal process with 2(2) spines.

Trichobothria. Palp: tarsi 8(8), tibia pd6(6) rd6(6). Leg I: tarsi 12(11), metatarsi 14(12), tibia pd8(7) rd5(6). Leg II: tarsi 12(10), metatarsi 13(11), tibia pd8(7) rd6(7). Leg III: tarsi 10(10), metatarsi 10(11), tibia pd6(5) rd6(7). Leg IV: tarsi 13(14), metatarsi 17(15), tibia pd8(8) rd8(8).

Leg spination. Spines absent from tarsi I and II. Leg I: metatarsi v01102(0011001); tibia v011112(010102), pd010(010). Leg II: metatarsi v001103(01203), pd0100(0100); tibia v01112(01112), pd00110(00110). Leg III:tarsi v00110(00110); metatarsi v8(9) scattered, d00020220(00020220); tibia v9(7) scattered, p0110(0110), r0001010(0001010); patella pd6(6) including 1(1) on distal edge. Leg IV: tarsi v5(5) scattered; metatarsi v11(11) scattered, rd00001000010(00001000010); tibia v6(6), rd0111110(0111110); femur pd13(13) in distal group.

Abdomen. Dorsum covered with fine bristles reduced to hairs on ventral surface.

Female allotype (Figs 10-12). *Size*. Carapace length 8.33, width 6.19, height 3.25, post foveal height 2.00. Caput ratio 1.63. Abdomen length 12.00, width 7.55.

Colour. Abdomen dorsum with distinct pattern of pale yellow bands in bilateral series. Venter as in male.

Carapace. Posterior edge with mid indentation. Edge fringed with fine hairs which encroach onto posterior half of post foveal surface. Striae glabrous and well defined. Line of 12 median bristles occupies length of caput arch. Fine golden hairs extend into the fovea. Group of 9 anteriorly inclined bristles between PME; a group of 13 posteriorly inclined bristles in front of AME. Fovea width 1.60, slightly procurved, almost straight.

Eyes. Placed on a low mound; anterior width 1.24, posterior width 1.14, length 0.79. Line joining the posterior edges of ALE transects the anterior fifth of AME. Posterior row recurved in front, strongly recurved behind.

Chelicerae. Rastellum with first row of 6(5) short strong spines, disordered second row of smaller spines and a few spines along prolateral cheliceral edge. Fang groove with 12(10) large promarginal teeth and 16(16) small teeth in retromarginal/ intermediate row beginning adjacent to third (fourth) distal promarginal tooth and extending 1 tooth beyond proximal promarginal tooth.

Labium. Length 1.03, width 1.44, separated from sternum by deep narrow suture which expands laterally.

Maxillae. About 59(65) anteroental fusiform cuspules.

Sternum. Length 4.35, width 3.68.

Legs. Limb measurements: leg formula – 4 1 2 3. Width of patella I, 1.32; tibial index leg I, 19.58. Width of patella IV, 1.63; tibial index leg IV, 19.33.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Palp	4.47	2.61	2.45	–	2.68	12.21
I	5.75	3.49	3.25	2.71	1.78	16.98
II	4.88	3.14	2.71	2.53	1.65	14.91
III	3.88	2.55	1.83	2.32	1.57	12.15
IV	5.62	3.49	4.94	4.16	2.06	20.27

Dense scopula complete on tarsi of palps and legs I, incomplete on metatarsi of legs I, restricted to prolateral and ventral surfaces of tarsi II and distal prolateral and ventral surfaces of metatarsi II. Scopula absent on retrolateral surfaces of legs II.

Trichobothria. Palp: tarsi 11(10), tibia pd7(7) rd6(6). Leg I: tarsi 13(11), metatarsi 14(13), tibia pd7(7) rd7(7). Leg II: tarsi 12(12), metatarsi 16(15), tibia pd7(8) rd7(8). Leg III: tarsi 10(10), metatarsi 10(9), tibia pd7(7) rd7(7). Leg IV: tarsi 14(12), metatarsi 15(16), tibia pd8(8) rd8(8).

Leg spination. Palp: tarsi pv0100(0100), rv010000(010000), plus about v12(12) divergent subproximal long bristles; tibia v0223(0223). Leg I: metatarsi v0102(0102); tibia v01110(0110). Leg II: tarsi rv01010(01010); metatarsi rv012(013); tibia v01110 (01110). Leg III: tarsi v9(7) scattered; metatarsi v023(023), pd00210(011110), rd001110(001110); tibia v023(023), pd0110(010), rd0110(0110); patella pd5(6) including 1(1) on distal edge. Leg IV: tarsi v15(17) in scattered group; metatarsi v10(11) in scattered group, rd001010(001010); patella about pd16(16) in proximal cluster; femur about pd23(25) in distal cluster.

Abdomen. With cover of fine hairs. Dorsum with median band of fine dark bristles.

Genitalia. Sclerotised lip of epigynum gently recurved, almost straight. Spermathecae in paratype KS22343 consist of a pair of bulbous vesicles which gradually enlarge terminally (Fig.12).

Etymology. The species is named in recognition of the author's eldest son, Derek Wishart.

Distribution and natural history. This trap-door spider's distribution extends from Farmeadow and Berry, northwards through Willowvale and Gerringong to Kiama and Minnamurra Falls. It is found in rainforest and urban situations.

The burrow entrance has not been observed in the wild. Burrows have been excavated as a result of systematic digging through a forest floor area, also by slicing off the soil surface of the forest floor and accidentally whilst gardening. In captivity the entrance is tubular, not funnel-shaped, about 10 mm diameter and with attached small pieces of vegetation; the opening is parallel with the ground. The lip is not rigid and may be folded inwards as a seal. In the wild the burrow is usually about 25 cm deep and lined with a continuous fragile silk tube which terminates

immediately before a soft but strong sock 3.5 cm long in which the spider, sometimes with spiderlings, is often found.

Mature males wander during April and May of each year.

Misgolas kirstiae n.sp.

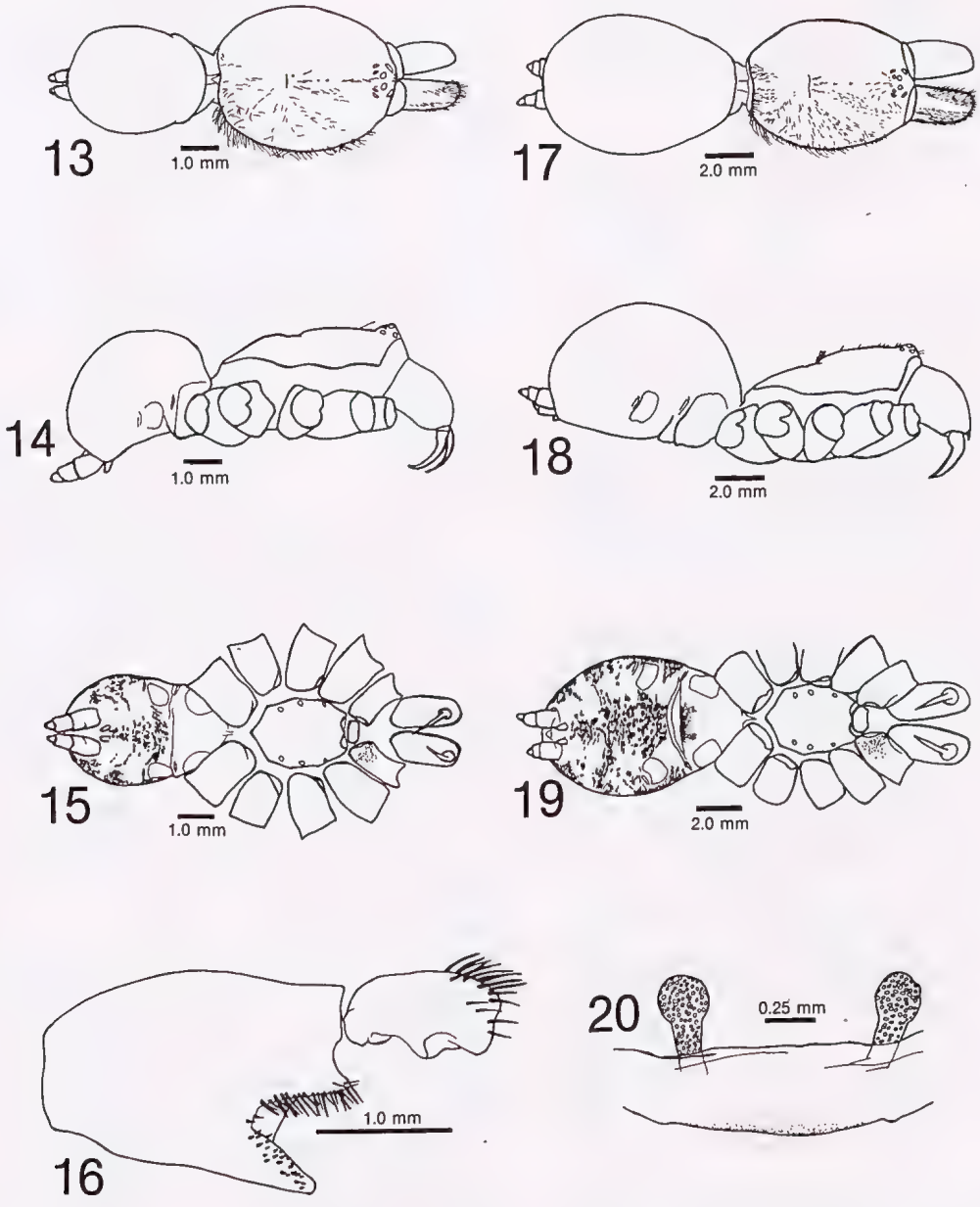
Figs 13-20, 32,33

Material examined. HOLOTYPE, male, KS22355(AM). "Scalloway", Willowvale, near Gerringong, NSW (34°44'11"S 150°47'23"E), 6 Nov. 1985, GW.

ALLOTYPE, female, KS22356(AM). Locality as above, 5 Oct. 1988, GW, maintained alive until 23 Jan. 1989 and then taken with 55 spiderlings and preserved.

PARATYPES (all AM, locality as above and collected GW). Males: KS22357 to KS22367, 19 Sept. 1985, 9 Nov. 1985, 15 Oct. 1986, 23 Sept. 1987, 23 Oct. 1985, 23 Sept. 1985, 20 Oct. 1985, 31 Oct. 1985, 14 Nov. 1985, 17 Oct. 1986, 3 Nov. 1987. Females: KS22368 to KS22370, 17 Mar. 1988 (genitalia dissected), 8 Dec. 1985, 10 Oct. 1986.

Diagnosis. Small brown spiders; reflective hairs and numerous black hairs on carapace. Carapace length in female 5.5-7.5, in male 5.1-6.4. Eyes on a tubercle. Venter of abdomen pale with dark brown pattern (Figs 15,19). Fangs with keel on prolateral edge. Maxillary cuspules extend from anteroental area almost to posteroental angle. Intermediate row of cheliceral teeth absent. Male palpal tibia without a distal hooked apophysis (Fig.16); embolus slender and sinuous with retrolateral lamina with 1 pronounced fold, apophysis



Figs 13-20. *Misgolas kirstiae* n.sp.: 13-16, male holotype. 13, body dorsal; 14, body lateral; 15, body ventral; 16, right palpal tibia and cymbium retrolateral. 17-19, female allotype. 17, body dorsal; 18, body lateral; 19, body ventral. 20, female paratype KS22368 internal genitalia dorsal.

absent (Figs 32,33).

Male holotype (Figs 13-16,32,33). *Size*. Carapace length 5.19, width 4.09, height 1.33, post foveal height 1.10. Caput ratio 1.24. Abdomen length 4.00, width 3.02.

Colour. Light tan; carapace, legs and chelicerae unicolourous except some lateral surfaces of palps and legs I and II with very slightly darker smudges; carapace in life with hirsute sheen. Abdomen dorsum dark brown with precise transverse yellow bands in bilateral series of 8. Venter pale with characteristic dark brown median pattern extending from epigastric furrow to PMS (Figs 15,19).

Carapace. Ovate. Edge evenly fringed with black bristles which encroach uniformly onto all interstrial areas; posterior edge recurved. Striae glabrous. Line of 9 median bristles on very low, almost flat caput arch. 2 pairs of foveal bristles are anteriorly inclined. Group of 6 anteriorly inclined bristles between PME; group of 6 posteriorly inclined bristles in front of AME. Fovea very short, 0.52 wide, straight. Clypeus and ocular area extended anteriorly.

Eyes. Compact on a tubercle, lateral eyes on sides of tubercle facing horizontally. Anterior and posterior widths equal, 0.93; length 0.59. Line joining posterior edge of ALE passes marginally inside AME; posterior eyes straight in front, recurved behind. Tapetum of ALE, PME and PLE highly reflective.

Chelicerae. Light tan, not heavily pigmented. Rastellum a single row of 10(14) long weak spines and spinules. Pallid compact intercheliceral tumescence is sparsely covered with some short setae. Fang groove with 6(7) promarginal teeth and 4(3) smaller retromarginal teeth beginning adjacent to the fourth(sixth) distal promarginal tooth and terminating adjacent to the proximal promarginal tooth; intermediate row absent. Fangs armed with a thin translucent keel suspended along the prolateral edge.

Labium. Length 0.41, width 0.72. Separated from sternum by centrally divided suture. Cuspules absent.

Maxillae. About 61(65) cuspules placed anteroentally and extending almost to posteroental angle. Most cuspules fusiform, some elongate and pointed and few surmounted by fine hair.

Sternum. Length 2.71, width 2.04. Anterior sigilla small, round and close to margin, middle and posterior sigilla larger, round and more distant from margin.

Legs. Limb measurements: leg formula – 4 1 2 3. Width of patella I, 0.90; tibial index leg I, 15.93. Width of patella IV, 0.88; tibial index leg IV, 13.07.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Palp	2.79	1.39	2.43	–	1.11	7.72
I	4.59	2.42	3.25	3.68	2.16	16.10
II	4.31	2.17	2.97	3.21	1.99	14.65
III	3.84	1.88	2.61	3.33	1.99	13.65
IV	4.94	2.40	4.31	4.66	2.40	18.71

Palp (Fig.16) with apical row of weak elongate sharp spines, receding and reduced to spinules over the distal quarter of dorsal surface of cymbium. Palpal tibia with large retroventral apophysis covered dorsally with spines; ventral surface of tibial excavation with band of long spines; apical hooked apophysis absent. Bulb with retrolateral embolic flange with one pronounced fold; embolus arched, slender and sinuous, apophysis absent. Weak scopula present on tarsi and metatarsi of legs I, incomplete on legs II and III and almost absent on legs IV. Tibia I with apical bifid apophysis; distal process with 3(2) spines and proximal process with 3(2) spines.

Trichobothria. Palp: tarsi 8(7), tibia pd6(5) rd6(6). Leg I: tarsi 9(10), metatarsi 11(10), tibia pd7(7) rd6(6). Leg II: tarsi 10(10), metatarsi 11(10), tibia pd7(6) rd6(6). Leg III: tarsi 12(12), metatarsi 11(11), tibia pd7(6) rd6(6). Leg IV: tarsi 10(10), metatarsi 11(12), tibia pd9(8) rd7(7).

Leg spination. Spines absent from all tarsi. Scopula on tarsi III and IV progressively displaced by about 15 to 20 scattered ventral bristles. Leg I: metatarsi v012(012); tibia v01112(01112), p010(010); patella pd00110(00110). Leg II: metatarsi v01102(01102), p0100(0100); tibia v01112(01112), p01111(01111); patella pd0110(0110). Leg III: metatarsi v01203(00203), d002120(002120); tibia v0112(0112), pv0011(0001), pd0110(0110), rd01110(01110); patella pd01110(group of 5 none on distal edge). Leg IV: metatarsi v10(10), rd0010110(0010010); tibia v9(11), rd001110(001110).

Abdomen. Dorsum with distinct pattern of bilateral transverse bands and covered with long bristles. Sides and ventral surfaces covered with long fine hairs.

Female allotype (Figs 17-20). *Size*. Carapace length 7.45, width 5.87, height 2.27, post foveal height 1.61. Caput ratio 1.42. Abdomen length 8.53, width 6.19.

Colour. Medium tan otherwise as for male.

Carapace. Ovate. Edge fringed with fine dark bristles which encroach onto all interstrial areas. Line of nine small median bristles occupies the full length of very low caput arch. About 5 pairs of anteriorly inclined foveal bristles emerge from the fovea. Group of 13 anteriorly inclined bristles between PME; group of 8 posteriorly inclined bristles in front of AME. Fovea 0.98 wide, procurved. Clypeus and ocular area extended anteriorly beyond base of carapace as for male.

Eyes. Compact, on small tubercle, arranged as for male. Anterior width 1.26, posterior width 1.16, length 0.74. Line joining posterior edge of ALE transects the anterior third of AME. Posterior row straight in front, recurved behind.

Chelicerae. Medium tan, not heavily pigmented. Rastellum single row of 10(9) long weak spines and spinules. Fang groove with 7(7) promarginal teeth and 5(7) smaller retromarginal teeth beginning adjacent to fifth(fifth) distal promarginal tooth and extending 1(1) tooth beyond proximal promarginal tooth.

Labium. Length 0.77, width 1.24.

Maxillae. About 65(64) fusiform cuspules placed anteroentally and extending to posteroental angle.

Sternum. Length 4.00, width 3.02. Three pairs of sigilla all small, round and approximately equidistant from margin.

Legs. Limb measurements: leg formula 4 1 2 3. Width of patella I, 1.24; tibial index leg I, 19.97. Width of patella IV, 1.37; tibial index leg IV, 18.08.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Palp	4.00	2.40	2.30	–	2.32	11.02
I	5.19	3.21	2.99	2.53	1.47	15.39
II	4.81	2.99	2.58	2.43	1.39	14.20
III	4.11	2.63	2.22	2.55	1.50	13.01
IV	5.63	3.33	4.23	4.12	1.88	19.19

Scopula present on palpal tarsi and tarsi and metatarsi of legs I and II; sparse on leg II, absent on legs III and IV.

Trichobothria. Palp: tarsi 9(9), tibia pd6(6) rd6(6). Leg I: tarsi 12(11), metatarsi 12(12), tibia pd7(7) rd6(6). Leg II: tarsi 12(12), metatarsi 14(15), tibia pd7(7) rd6(6). Leg III: tarsi 14(13), metatarsi 16(16), tibia pd7(7) rd7(7). Leg IV: tarsi 12(11), metatarsi 17(14), tibia pd8(9) rd7(8).

Leg spination. Palp: tarsi v0200(0200) plus about 12(12) apically inclined subproximal ventral bristles; tibia v02203(02203), patella pv010(010). Leg I: tarsi about v17(20) bristles adjacent to unpaired claw; metatarsi v02102(01102), tibia v01112(01112), p01(01). Leg II: tarsi v00010(0010) plus about 22(22) bristles; metatarsi v011002(012002), p010(010); tibia v01112(01112), p0110(0110). Leg III: tarsi v3(3) plus about 35(40) bristles along ventral length; metatarsi v011002(012002), d022(022); tibia v01112(01112), p0110(0110), r0000(0010); patella pd00110(001110). Leg IV: tarsi v10(8) plus about 30(30) bristles along ventral length; metatarsi v11(10) in scattered group, rd0010110(0010110); tibia v020212(020212), r0110(0110).

Abdomen. Dorsum covered with fine dark bristles and fuscous hairs. Setae finer on venter.

Genitalia. Sclerotised lip of epigynum straight; spermathecae divergent. Spermathecae in paratype KS22368 pair of short vesicles each with terminal sphere (Fig.20).

Etymology. The species is named in recognition of the author's eldest daughter, Kirstie Wilson.

Taxonomic remarks. This spider possesses several unusual characters and the question is raised as to whether it should be placed in a new genus. Because the distribution of maxillary cuspules is extensive along the length of the ental surface, an intermediate row of cheliceral teeth is absent, leg markings are greatly reduced, the caput ratio is very low and the carapace is more ovate than elongate there is some basis for a new genus to be raised to accommodate this spider. This proposal is further supported by the uniform cover of fine dark bristles over the carapace, the eyes compactly placed on a distinct tubercle, the short fovea width relative to the width of the carapace, the rastellum spines reduced to long spinules and bristles (as also are all leg and palp spines), the absence of a distal hooked apophysis with a terminal tuft of short spines from the male palpal tibia, and the slender, sinuous embolus of the male bulb that lacks a small apophysis.

Argument favouring the retention of *M. kirstiae* within the genus *Misgolas* is that the unusual characters may not have great weighting, or are not in conflict with the most recent diagnosis for the genus (Main, 1985 and personal communication) and the proposed new genus would contain but one species and so require a more definite gap (Mayr, 1969) between it and other genera within the Idiopidae. This question should be resolved when a complete revision of the genus can be undertaken, when many more of the species yet to be described are more fully examined and a better appreciation is gained of the variation within it.

Distribution and natural history. The only records of this spider are from the type locality in a remnant rainforest patch. The burrow in the natural habitat is not known. Spiders have been found in removed soil sometimes encased in a soft fragile silken sock about 3 cm long and heavily impregnated with soil. In captivity the entrance of the burrow is sealed by a half-moon shaped flap.

Mature males wander during September, October and November of each year.

Misgolas robertsi (Main & Mascord, 1974)

Figs 21-24, 34,35

Dyarcyops robertsi Main & Mascord, 1974: 15-21.
Misgolas robertsi.–Main, 1985a: 34, 53, 57.

Material examined. HOLOTYPE, female, KS12(AM). Minnamurra Falls, Kiama, NSW, 12 Oct. 1964, R.M. Mascord. PARATYPES, females, KS13(AM). Minnamurra Falls, Kiama, NSW, Apr. 1965, R. Mascord (genitalia dissected).

Other material (all AM). Males: KS22371 to KS22381. All "Scalloway", Gerringong, NSW (34°44'11"S 150°47'23"E), 2 May 1986, 17 Apr. 1986, 11 Nov. 1986, 7 May 1987, 20 Apr. 1987, 25 Nov. 1985, 6 Jan. 1987, 10 Jan. 1987, 6 Apr. 1987, 29 Apr. 1987, 26 May 1987. Females: KS22382 to KS22389. All "Scalloway", Gerringong, 14 Jan. 1986, 14 Feb. 1986, 24 Apr. 1986, 7 Feb. 1987, 12 Feb. 1987, 10 May 1987, 2 July 1987, 30 Oct. 1988. All collected GW.

Diagnosis. Medium sized brown spider; dorsum of abdomen with distinct pattern of 8 yellow transverse bands; venter pale with dark brown median band (Figs 23,24). Female carapace length 7.5-11.3. Male carapace length 7.5-8.1. Embolus of male bulb with retrolateral flange with about 8 folds; small right angled triangular apophysis is placed dorsally about halfway along embolus (Figs 34,35).

Female holotype KS12(AM), (Fig.24). A supplementary description is given here of the holotype of *Dyarcyops robertsi.*

Carapace height 3.44, post foveal height 1.63. Caput

ratio 2.11. Carapace with fuscous hairs extending to fovea and fringed with hairs encroaching onto posterior half of post foveal area; posterior edge recurved. Line of 7 median bristles occupies caput arch. Line of about 5 small bristles placed prolaterally adjacent to each anterior stria and terminates at foveal edge. Fovea width 1.81; slightly procurved. Group of about 13 bristles between and behind PME; group of 5 posteriorly inclined bristles in front of AME. Eyes placed on low mound. Venter pale with dark brown median band extending from epigastric furrow to PMS. Chelicerae with rastellum of first row of 7(6) short teeth, second row of 11(8) teeth and about 4(5) in disordered third row.

Leg spination. Palp: tarsi pv1(0) sub proximal, rv0100(0); tibia pv7(7), rv7(6); patella pd11(0). Leg 1: metatarsi rv missing(010001), tibia v0111111(0111111). Leg II: metatarsi v011003(011003); tibia v0011111 (011011). Leg III: tarsi v6(4) in scattered group; metatarsi v012(013), d0002120(0002020); tibia v00202(01202), pd00110(00110), rd00101(00101); patella pd11(11), nil(nil) on distal edge. Leg IV: tarsi v15(15), in scattered group; metatarsi v10(9) in scattered group; femur dense group of about pd40(40) along distal edge.

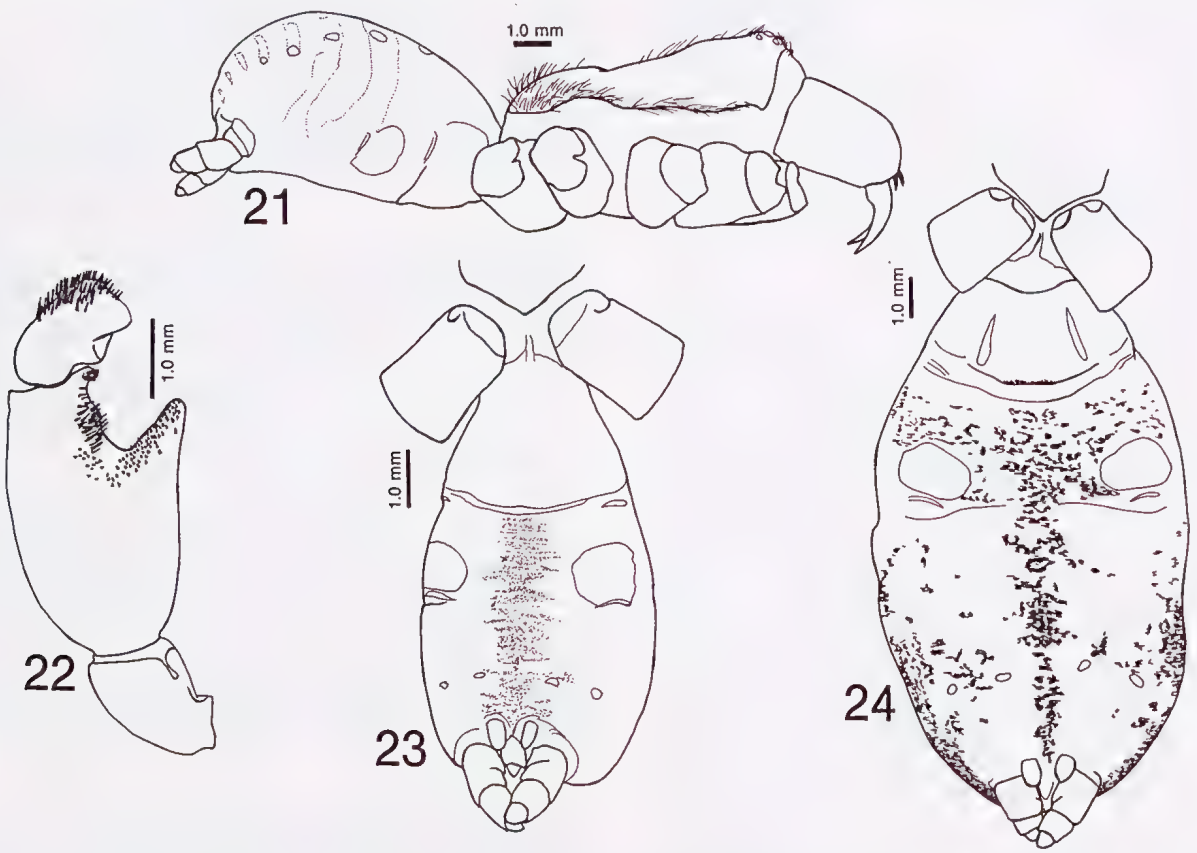
Trichobothria. Palp: tarsi 13(13), tibia pd8(9) rd8(8). Leg I: tarsi missing(15), metatarsi missing(15), tibia pd9(10) rd7(8). Leg II: tarsi 15(14), metatarsi 15(15), tibia pd9(10) rd8(8). Leg III: tarsi 14(14), metatarsi 12(12), tibia pd9(8), rd9(9). Leg IV: tarsi 13(13), metatarsi 16(16), tibia pd10(9), rd10(9). Sclerotised lip of epigynum recurved with broad extended medial indentation.

Description of male KS22371(AM), (Figs 21-23,34,35). *Size.* Carapace length 7.55, width 6.03, height 2.08, post foveal height 1.49. Caput ratio 1.40. Abdomen length 8.18, width 4.88.

Colour. Generally dark brown, carapace bedecked with golden hirsute sheen. Prominent dark brown blotch on retrolateral distal surface of palpal patella, prolateral distal surface of tibia I, full length of both lateral surfaces of patella I and patella II and full length of retrolateral surface of patella III. Abdomen dorsum dark brown with precise transverse yellow bands in bilateral series of 8. Venter pale with median dark brown band extending from epigastric furrow to PMS.

Carapace. Posterior edge recurved. Edge fringed with brown bristles which encroach onto posterior half of post foveal surface. Striae glabrous. Line of 10 median bristles occupies almost straight caput arch. Line of small bristles and fine golden hairs prolaterally adjacent to each anterior stria and terminates at foveal edge. Group of about 14 anteriorly inclined bristles between PME; group of about 9 bristles in front of AME. Fovea 1.39 wide, slightly recurved.

Eyes. Median eyes placed on low tubercle; lateral eyes on tubercle edge; anterior width 1.23, posterior width 1.15, length 0.72. Line joining posterior edge of ALE passes marginally inside AME; posterior eyes



Figs 21-24. *Misgolas robertsi* (Main & Mascord): 21-23, male specimen KS22371. 21, body lateral; 22, right palpal tibia and cymbium retrolateral; 23, abdomen ventral. 24, female holotype abdomen ventral.

procurved in front, almost straight behind.

Chelicerae. Rastellum with first row of 7(6) long teeth and second row of 5(6) shorter teeth. Pallid elongate intercheliceral tumescence extends beyond half length of chelicera and is sparsely covered with short setae. Fang groove with 7(7) promarginal teeth and 13(11) smaller retromarginal/intermediate teeth beginning adjacent to between third and fourth distal promarginal teeth and terminating 2(0) teeth beyond proximal promarginal tooth.

Maxillae. About 49(47) anteroental small cuspules of which most are fusiform but apically pointed; a few cuspules are surmounted by a fine hair and some are tapered apically to form short spiniform cuspules.

Sternum. Length 4.19, width 2.97. Anterior sigilla small, ovate submarginal; middle and posterior sigilla progressively larger and distant from margin.

Legs. Limb measurements: leg formula – 4 1 2 3. Width of patella I, 1.26; tibial index leg I, 15.02. Width of patella IV, 1.39; tibial index leg IV, 13.65.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Palp	3.96	1.91	3.57	–	1.65	11.09
I	7.19	3.53	5.75	5.13	3.08	24.68
II	6.56	3.33	5.06	4.63	3.04	22.62
III	5.19	2.58	3.49	4.16	2.99	18.41
IV	7.37	3.37	6.81	6.19	3.53	27.27

Palp with dense cluster of skewer shaped spines evenly distributed over distal half of dorsal surface of cymbium. Tibia with large retroventral apophysis covered dorsally with very short spines; ventral surface of tibial excavation with median extended brush of long robust bristles and apical curved apophysis with a terminal tuft of long robust bristles. Bulb with retrolateral embolic flange with about 8 fine folds; embolus straight, not twisted, with small right angled triangular apophysis placed dorsally about halfway along embolus. Scopula dense on tarsi of legs I and II and sparse on legs III and IV. Tibia I with apical bifid apophysis; distal process with 3(3) spines and proximal process with 4(4) spines.

Trichobothria. Palp: tarsi 10(9), tibia pd7(7) rd6(7). Leg I: tarsi 14(14), metatarsi 13(14), tibia pd8(8) rd8(8). Leg II: tarsi 14(14), metatarsi 13(13), tibia pd8(8) rd7(8). Leg III: tarsi 12(12), metatarsi 11(10), tibia pd6(8) rd8(8). Leg IV: tarsi 13(13), metatarsi 14(14), tibia pd8(8) rd8(8).

Leg spination. Spines absent from all tarsi. Leg I: metatarsi v010(010); tibia v011112(011112). Leg II: metatarsi v010(011); tibia v01112(01112). Leg III: metatarsi v0112(0112), d002130(002120); tibia v02(02), p010(000), r011(011); patella pv7(10) including 1(1) on distal edge. Leg IV: metatarsi v8(6) scattered; tibia v011112(011112); femora pd22(19) in distal group.

Abdomen. Anterior band of dorsum pattern is represented by a single bare spot; bands II and III extend to venter each with central sigilla-like spot; bands IV and V terminate laterally at sigilla-like spot; each set of 5 spots arranged in lateral line; bands VI, VII and VIII posteriorly placed and reduced. Venter yellow with dark brown median band extending from epigastric furrow to PMS; 4 sigilla-like spots in transverse arc around spinnerets.

Distribution and natural history. This spider is usually restricted to rainforest remnant areas near Minnamurra and Gerringong but specimens have been collected from urban Kiama.

The aerial tube of the burrows of these spiders varies between 7 and 12 cm in height and is attached only at entrance level to a rock, tree trunk or stem; the silk material of the tube is thin but durable, impregnated with soil and sometimes small pieces of vegetation such as moss if nearby on the article of attachment and which give the appearance of growing on the tube. At ground level the tube material becomes thick and spongy and below ground it is fine and frail so that the aerial tube may be easily detached at the junction. Unattached to the end of the underground tube and usually at a depth of about 15 cm is a white sock about 4 cm long and 1 cm in diameter in which the spider is usually found. The silk lining of the sock is thin and renitent.

Mature males have been captured in the summer and autumn with the highest concentration in the latter period.

Misgolas mascordi n.sp.

Figs 25-27, 36,37

Material examined. HOLOTYPE, male, KS16(AM), Dorrigo State Park, Apr. 1972, C.E. Chadwick. Right Leg IV fractured, abdomen misshapen and partly blackened. Previously described as male paratype of *Dyarcyops robertsi* Main & Mascord (1974).

ALLOTYPE, female, KS22390(AM). The Glade, Dorrigo National Park, NSW (30°22'30"S 152°43'9"E), 8 Dec. 1987, Bruce Beaumont.

PARATYPE, female, KS22391(AM). The Glade, Dorrigo National Park, NSW, 8 Dec. 1987, (genitalia dissected) GW.

Diagnosis. Medium sized brown spider. In female, carapace in life with abundant cover of reflective golden hairs, length up to 11.5; hairs, especially on proximal segments of palp and legs I and II, long whisker-like. Venter with dense even dark brown speckles on anterior half (Fig.25). In male carapace with sparse covering of reflective golden hairs, length 7.5; embolus of male bulb bilaterally flanged, the embolus appearing flat and blunt (Figs 36,37).

Male holotype (Figs 36,37). Main & Mascord (1974: 18-21) described this male as the paratype of *Dyarcyops robertsi*; a supplementary description is given here.

Carapace height 2.31, post-foveal height 1.50. Caput ratio 1.54. Carapace and all femora even dark brown. Carapace with sparse fuscous hairs which do not extend to fovea and fringed with bristles which encroach onto posterior half of post foveal surface; posterior edge slightly recurved, almost truncate. Line of 10 median

bristles occupies low caput arch and terminates at foveal edge. Line of about 9 small bristles placed prolaterally adjacent to each anterior stria and terminates at foveal edge. Fovea width 1.16; slightly recurved. Group of 12 bristles lies behind PME; single long posteriorly inclined bristle and several much smaller bristles in front of AME. The eyes lie on low tubercle; line joining posterior edge of ALE bisects AME. Posterior eyes straight. Abdomen has prominent sigilla-like glabrous spot on each distal edge of 5 pairs of narrow transverse dorsal bands. Venter pattern obscure appearing pale on anterior half darkening posteriorly, dark brown adjacent to spinnerets; 4 sigilla-like spots arranged in transverse retrocurve near spinnerets. Chelicerae with rastellum of single row of 7(8) robust spines and disordered incomplete second row. Pallid crescent-shaped intercheliceral tumescence is covered with procumbant setae becoming sparse distally.

Leg spination. Spines absent from all tarsi. Leg I: metatarsi v0012000(0212000); tibia v011211(011111). Leg II: metatarsi v01210(00310); tibia v011111(011212). Leg III: metatarsi v022(00212), d0022020(0021020); tibia v0222(0222), p01010(01010), r011(011); patella pd5(5) nil on distal edge. Leg IV: metatarsi pv01101012(00111012) plus several stout bristles, femur pd6(6) plus several strong bristles along distal edge.

Trichobothria. Palp: tarsi 11(10), tibia pd6(6) rd4(4). Leg I: tarsi 13(12), metatarsi 14(15), tibia pd7(7) rd7(7). Leg II: tarsi 12(12), metatarsi 13(14), tibia pd7(8) rd7(7). Leg III: tarsi 12(12), metatarsi 10(10), tibia pd6(6) rd7(7). Leg IV: tarsi 12(12), metatarsi 14(16), tibia pd8(8) rd8(8). Palpal bulb with retrolateral embolic flange with seven folds; flange narrows and continues along embolus; prominent fold of prolaterally placed secondary flange is positioned about halfway along embolus, the flange continuing with a torn-like edge. The bilaterally flanged embolus appears flat and broad; distal tip of embolus spoon-like, orifice dorsal (Figs 36,37).

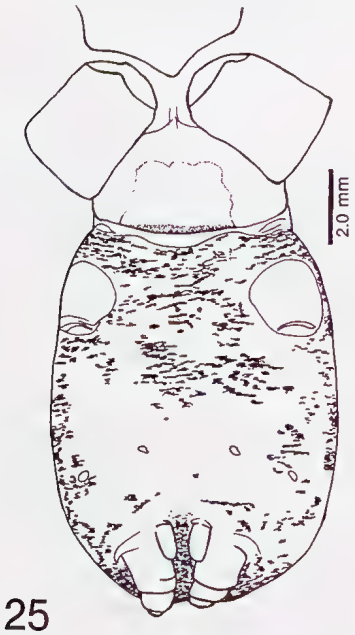
Female allotype (Figs 25-27). *Size.* Carapace length 10.78, width 7.64, height 4.02, post foveal height 2.06. Caput ratio 2.68. Abdomen length 12.46, width 7.74.

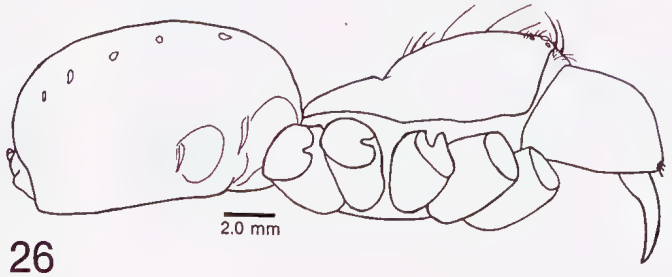
Colour. Generally light brown, carapace in life with thick golden hirsute sheen. Limbs with darker lateral longitudinal bands coinciding with hirsute areas. Abdomen dorsum pale with dark brown maculation, bilateral bands absent; venter dark with a dense evenly distributed dark brown speckle on anterior half (Fig.25).

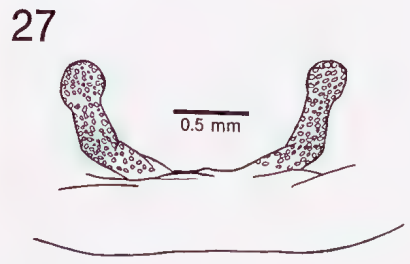
Carapace. Posterior edge with medial indentation. Edge fringed with fine hairs becoming larger posteriorly and encroaching onto most of post foveal surface. Striae glabrous and well defined. Line of 6 median bristles occupies low caput arch. Line of smaller bristles is placed prolaterally adjacent to each anterior stria and terminates at foveal edge. Group of 13 bristles between PME; single long anteriorly directed bristle with several smaller bristles between AME. Fovea 2.09 wide, straight.

Eyes. AME placed on low mound; anterior width 1.82, posterior width 1.57, length 0.88. Line joining posterior edge of ALE transects anterior quarter of AME. Posterior eyes slightly recurved in front, straight behind.

Chelicerae. Rastellum with first row of 6(7) robust spines, second row of 9(9) and a few further small spines retreat along the prodorsal cheliceral edge. Fang groove with 8(8) large promarginal teeth and 17(17) smaller retromarginal/intermediate row teeth beginning adjacent to third distal promarginal tooth and terminating







Figs 25-27. *Misgolas mascordi* n.sp.: 25-26 female allotype. 25, abdomen ventral; 26, body lateral. 27, female paratype KS22391 internal genitalia dorsal.

two teeth beyond the proximal promarginal tooth.

Labium. Length 1.22, width 1.81, separated from sternum by broad suture.

Maxillae. About 60(65) anteroental fusiform cuspules.

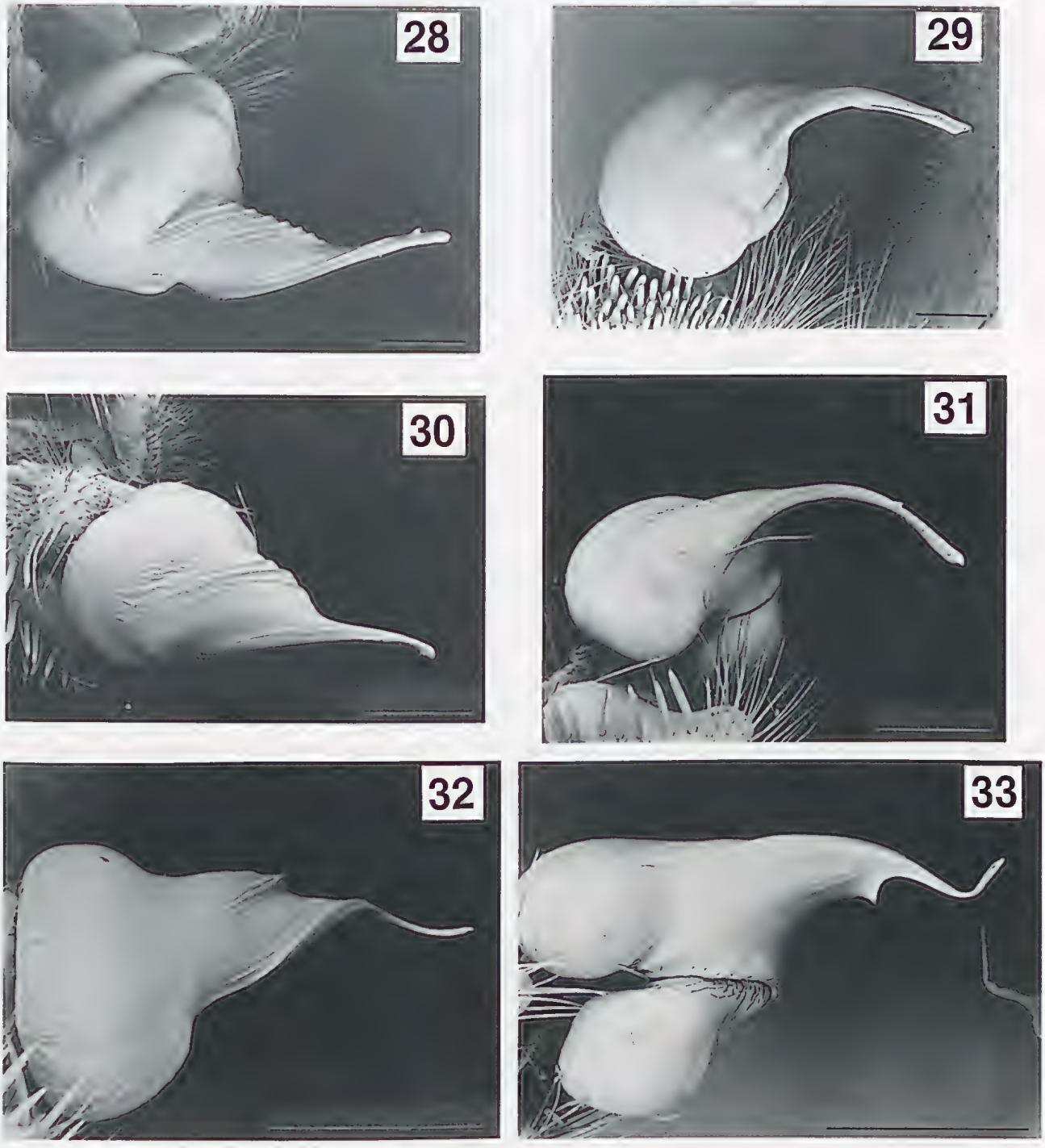
Sternum. Length 5.57, width 4.62. Anterior sigilla small, round, submarginal; middle and posterior sigilla progressively more ovate, larger and distant from margin.

Legs. Limb measurements: leg formula – 4 1 2 3. Width of patella I, 1.78; tibial index leg I, 18.90. Width of patella IV, 1.91; tibial index leg IV, 19.67.

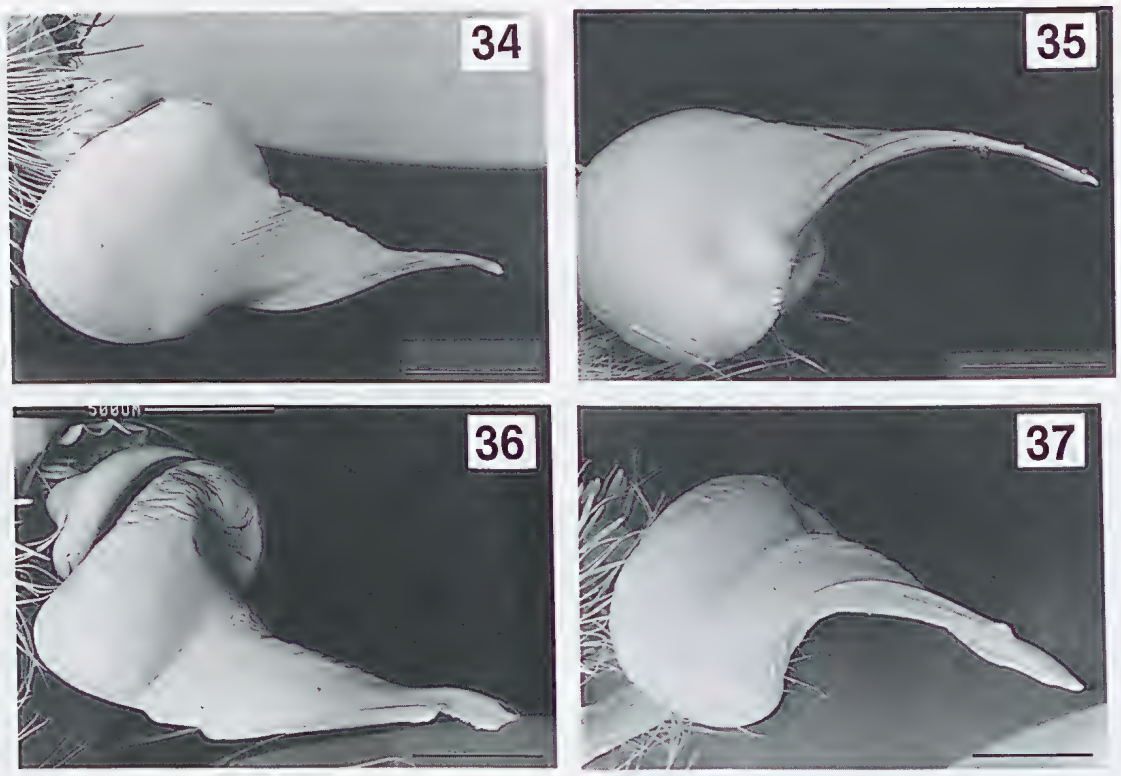
	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Palp	6.12	3.18	3.37	–	3.80	16.47
I	7.55	4.55	4.87	4.00	2.19	23.16
II	6.38	4.08	3.88	3.45	2.01	19.80
III	4.81	3.10	2.40	2.97	1.86	15.14
IV	7.06	4.08	5.63	4.88	2.17	23.82

Dense scopula complete on tarsi of palps and legs I and II. Incomplete on metatarsi of legs I and II.

Trichobothria. Palp: tarsi 11(11), tibia pd7(7) rd8(8). Leg I: tarsi 14(25), metatarsi 19(20), tibia pd10(10) rd7(6). Leg II: tarsi 15(15), metatarsi 16(16), tibia pd8(8)



Figs 28-33. 28-29 - *Misgolas hubbardi* n.sp. male paratype KS22316 right bulb: 28, dorsal; 29, prolateral; 30-31 - *Misgolas dereki* n.sp. male paratype KS22342 right bulb: 30, dorsal; 31, prolateral; 32-33 - *Misgolas kirstiae* n.sp. male paratype KS22361 right bulb: 32, dorsal; 33, ventral. Scale bars: 0.5 mm.



Figs 34-37. 34-35 - *Misgolas robertsi* (Main & Mascord): male specimen KS22375 right bulb: dorsal; 35, prolateral; 36-37 - *Misgolas mascordi* n.sp. male holotype (paratype of *Dyarcyops robertsi* Main & Mascord KS16) right bulb: 36, dorsal; 37, prolateral. Scale bars: 0.5 mm.

rd8(8). Leg III: tarsi 13(12), metatarsi 13(13), tibia pd8(7) rd8(8). Leg IV: tarsi 12(13), metatarsi 20(22), tibia pd9(9) rd9(10).

Leg spination. Palp: tarsi pv01000(01000), rv010000(010000); tibia pv011120(011120), rv01110 (01110). Leg I: metatarsi pv010001(010002), r01001(01103); tibia pv01(01), rv011110(011110). Leg II: metatarsi pv01(01), rv0101(01101); tibia v011100(011110). Leg III: tarsus v4(4) scattered; metatarsi v013(023), pd0011010(0001010), rd0000010(0010110), tibia p0110(0110), r0110(0110), patella pd9(9) of which 1(1) is on distal edge. Leg IV: tarsi v11(10) scattered group; metatarsi v023(00213); patella prodorsal group of proximal bristles and small spines; femur pd40(40) short spines on distal edge.

Abdomen. Dorsum with 5 sigilla-like spots corresponding to those described from male. Venter with four sigilla-like spots arranged in a transverse row immediately anterior to the spinnerets.

Genitalia. Sclerotised lip of epigynum slightly recurved, medial indentation absent. Spermathecae in paratype KS22391 pair of long vesicles diverging at about right angles, each terminating in small sphere, trunks bent as if twisted (Fig.27).

Etymology. The species is named in recognition of the late Ramon Mascord, amateur arachnologist, photographer and collector.

Distribution and natural history. This spider is known only from the type locality, Dorrigo National Park, a subtropical rainforest with a high dense canopy.

The aerial tubes of the burrows, although very rare at the type locality, are conspicuously attached to the trunks or buttress roots of trees. The tube is up to 26 cm in height above ground, attached to its support only at the rear of the lip of the entrance, and is strong, especially at the base where the tube material is much thickened; it may be decorated with mosses (or other vegetative material) transplanted from the immediate vicinity in which case the support is bare of moss for about 5 cm either side of the tube. Below ground level the silk tube is very thin, extends to a depth of about 20 cm and terminates in a thin soft sock. The junction between the thick strong aerial tube and the thin subterranean tube is weak and easily broken. The burrow occupied by the allotype had the tube entrance sealed with the outer lip pulled inwards and secured by the application of silk; 10 cm below ground level a square white pillow shaped eggsac containing 283 eggs was attached to the silk lining of the burrow; the spider was secreted within the terminal sock.

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APPENDIX

Table 1. Comparative list of characters for some *Misgolas* species.

Misgolas species	Abdomen pattern dorsum; venter	Metatarsi IV, rd spines	Male tarsi v spines	Intercheliceral tumescence	Cymbium, apical spines	Male bulb, folds on flange; embolic apophysis
M. rapax	fine chevrons; absent	absent	absent	small; sparse setae on proximal half	peg-like	about 5; absent
M. hubbardi	indistinct; dense near spinnerets	absent	absent	small; ill-defined, covered with setae	peg-like	about 5; subdistal thorn shaped
M. dereki	distinct yellow bands; sparse speckle	2	present on legs III and IV	dark setae concentrated proximally	long, sparse	3; mid-placed, thorn shaped
M. kirstiae	distinct yellow bands; broad median band	absent	absent	compact; sparse short setae	long, weak	1 large fold; absent
M. robertsi	distinct yellow bands; narrow median band	absent	absent	elongate; short setae	skewer shaped, weak	about 8; mid-placed right angle shaped
M. mascordi	indistinct; dense on anterior half	absent	absent	crescent shaped; procumbant setae	needle-like	7; absent

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Extraordinary New Subterranean Isopods (Peracarida: Crustacea) from the Kimberley Region, Western Australia

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ABSTRACT. A new genus and two new species of fresh water isopods from ground waters of the Kimberley region of West Australia are described. This new genus cannot be immediately assigned to an isopod suborder or family because its unique combination of characters encompass many plesiomorphies, as well as synapomorphies with the 'Flabellifera' *sensu lato*. These features include free pleonites that are subequal except for an enlarged fifth pleonite, broad natatory pleopods, genital pores on medial extensions of the coxae, five pairs of oostegites, true coxal plates, an antennal protopod of three articles, and a rudimentary second flagellum on the antennula. One of the new species, well represented in one sample, is iteroparous and breeds continuously during the winter months. Because the type localities are from limestone fossil reefs not exposed to the marine environment since the Devonian period, these isopods may be remnants of an ancient freshwater stock. Name changes of some setal types are proposed.

WILSON, G.D.F. & W.F. PONDER, 1992. Extraordinary new subterranean isopods (Peracarida: Crustacea) from the Kimberley region, Western Australia. Records of the Australian Museum 44(3): 279–298.

During 1988, one of us (WFP) explored fresh water habitats in parts of the Kimberley Region of Western Australia, and made several incidental collections of small crustaceans from a pool in a limestone cave and in several springs issuing from limestone. This material contained odd, swimming isopods that, in their natural habitat, looked like syncarid crustaceans. Preliminary inspection suggested that these animals were related to phreatoicidean isopods. Subsequent study, however, has revealed that these specimens represent a novel taxon that cannot be comfortably classified in any suborder of the Isopoda. This paper provides a detailed description of two species of the new taxon, a preliminary evaluation of its morphological features, and a discussion of its possible affinities and biogeography. The following description of the genus provides features of potential phylogenetic significance. A diagnosis and phylogenetic definition, however, will be provided with a natural classification estimated using cladistic techniques (research in progress). The combination of character states possessed by this new taxon may have a significant impact on interpretations of the phyletic relationships of isopods, recently evaluated using cladistic techniques by Brusca & Wilson (1991). Because this research is still in

progress, the precise classification of this new taxon is left undecided. Nevertheless, this taxon may be distinct from all other isopods at the subordinal level.

Methods and Terminology

Field collections were made using a hand sieve in three localities (K1, K2, K5) and a dip net in one (K10). Temperature, pH and conductivity (in s cm^{-1} at 25°C) were recorded from each site. The field pH meter was not functioning well and consequently the recorded pH must be regarded as only approximate. Ellaway *et al.* (1990) describe the water chemistry of the region from which the samples were obtained. The material was fixed in 8% formalin buffered with excess $NaHCO_3$.

The following descriptions use the same descriptive methods, terminology, and format as described in Wilson (1989), except for the setal forms discussed below. In the phylogenetic discussion, "higher isopods" refers to the non-basally derived groups of the Isopoda: Oniscidea (including Calabozoidea), Valvifera, Anthuridea, Epicaridea, Gnathiidea and "Flabellifera" *sensu* Brusca & Wilson (1991). The early derived or "lower isopods" are the Phreatoicidea, Asellota and Microcerberidea.

Setal morphology, although not a central part of this description, may be more important once comparative studies are done. This paper marks a shift from Wilson (1989) in the terminology of some setal types. The name "broom seta" of Hessler (1970), a small presumed mechanoreceptor (see arrow from basis in Fig.6A), has not been widely accepted and does not provide an unambiguous portrayal of the setal type. This seta is most like an amphipod microtrich sensillum "type 1c" described by Oshel *et al.* (1988), although the isopod form can be larger than 25 m and sits on a distinctive pedestal, rather than in a recessed pore. J. Lowry (personal communication) has suggested the name "penicillate" seta (from the diminutive Latin word *penicillum* meaning painter's brush). In this paper, the descriptor "penicillate" will be used instead of the previous name "broom seta". Setal forms of previous papers named variously "unequally bifid seta" (Hessler, 1970) or "sensory spine" [sic] (Brandt, 1988) have names that do not describe their morphology accurately or unambiguously. Because these setae are neither "bifid" nor "spines", we propose that this setal form be called "sensillate setae", in reference to the enervated sensillum emerging distally on the seta. This type of seta varies from morphologically complex forms with spinules, setules or denticles to smooth, often robust setae with only a tiny distal sensillum. In such cases, the specific morphologies will be indicated (e.g., distally denticulate sensillate seta of the type found on the pereopods). Although this is lexically complex, a simpler classification of these setae is not immediately obvious owing to substantial morphological intergradation among the various types of sensillate setal decorations. We agree with Oshel & Steele (1988) who argue that the use of "spine" to describe setae confounds the ontogenetic and phylogenetic origins of both structures. Herein "spine" will be used *only* for simple epidermal outgrowths. Poore (1991) gives a similar opinion.

Taxonomy

Tainisopus n.gen.

Type species. *Tainisopus fontinalis* n.sp.

Etymology. *Tainisopus* refers to the flattened, elongate and flexible body of this new isopod genus. The name is derived from the Greek word *tainia* ('ribbon' or 'band'), and the Greek combining forms *iso* ('like'), and *pus* ('foot'), which together can be construed to mean 'ribbon isopod'.

Description. Isopoda with elongate, dorsoventrally flattened body having substantial lateral as well as dorsoventral flexibility. Head (cephalon + thoracomere 1) without functional eyes, unpigmented eye lobe projecting anterolaterally on head. Head only partially recessed into pereonite 1, without apparent cervical groove or interantennal rostrum; cephalic dorsal surface clearly demarcated from lateral surface by cuticular ridge; anterior ridge on anterior face between antennulae connecting ventrally to bulbous rounded projection between antennae just dorsal to clypeus. All pereonites and pleonites approximately equal sized, except for distinctly larger pereonite 1 and pleonite 5. Pleotelson (urosome + telson) distinct, broad, flattened, lacking clear boundary between uropodal insertions and remainder of pleotelson. Pleotelson with ability of flexing at right angles to body axis. Anus subterminal, situated just posteromedial to uropodal insertions.

Female oopore on ventrolateral margin of coxa 5. Male genital papillae (penes) broad, flattened, articulated to triangular medial extensions of seventh coxae by broadly flexible region (not on separate sclerite).

Antennulae emerging near cephalic midline; article 1 with pronounced lateral curve; article 3 bearing rudimentary second flagellum consisting of single setose article on anteromedial side of distal margin. Antenna peduncle with 6 articles, basal article large and distinct, article 3 with scale fused.

Mandible incisor process curved and toothed; left mandible with flattened toothed lacinia mobilis; right mandible with modified, lacinia-like spine with multiple spinose projections adjacent to incisor process; spine row on ridge between incisor process and mandible; molar process truncate with broad triturative surface; large 3-articled palp with well-developed cleaning setae (curved setae with 2 rows of denticles grading into

setules distally) on 2 distal articles; dorsal condyle short, rounded and curved.

All pereopods with coxal plates (as defined by Brusca & Wilson, 1991); coxal plates of pereopods I-III completely or partially fused to produced and flattened lateral margins of body; coxal plates of pereopods IV-VII freely articulated with body dorsally along broad insertions. Coxal plate of pereopod VII of male covering most of ventral surface of pereonite 7, with penes attaching to posteromedial projections of coxa. Pereopods I-III subchelate and prehensile, with robust toothed sensillate setae on ventral margins of propodus (PI), carpus (PI-III), and merus (PI); coxae of pereopods I-III fused to lateral margins of body. Pereopods IV-VII with fewer robust sensillate setae on ventral margins and more walking leg-like. Fully-functional oostegites on coxae of pereopods I-V.

Pleopods I-V similar in shape. Pleopodal protopods broad with wide lateral margins bearing elongate sensillate setae, and medial projections bearing several curved setulate setae. Pleopodal exopods broad, rounded, with 2 large distinct articles, with many marginal plumose setae. Exopods of pleopod V covering anus. Endopod of pleopod I (both sexes) small, narrow, shorter than exopod, bluntly pointed or rounded distally, with medial setae. Endopod of male pleopod II elongate, longer than exopod, broad at base, narrowing to bluntly pointed tip having cuticular combs on medial margin. Endopods of pleopods III-V in male and of pleopods II-V in female shorter than exopod, completely lacking setae, trilobed, with central lobe thickest.

Uropods only slightly flattened, with broad elongate protopod having robust sensillate setae on lateral and medial margins and distally rounded rami. Endopod larger than exopod, both furnished with robust sensillate setae.

Remarks. *Tainisopus* differs from all other described isopods as currently defined in having the following characters. The antennula bears a rudimentary secondary flagellum, and the antenna has a basal article on the protopod, making it three-articled. Both of the features are found in other isopods (Flabellifera *sensu stricto* and Asellota, respectively), but no other isopod has both together. The penes are born on triangular medial projections of coxa of pereopod VII. This unusual feature may not occur in other isopods, although it could be related to the penial forms in the Asellota (Just & Poore, 1992). The flabelliferan-like features include broad natatory pleopods, a pereopodal tagmosis of three anterior grasping limbs and four posterior ambulatory limbs (see Brusca & Wilson, 1991), true coxal plates with the three anterior coxae fused to body. However, because these are generalised features found in many families, they do not advise us on the correct classification of *Tainisopus*. The detailed form of the pleopodal endopods is also unusual and not precisely typical of any other isopod group.

Tainisopus fontinalis n.sp.

Figs 1-8, 13, 14

Etymology. *Fontinalis*, meaning 'from a spring' (Latin), refers to the habitat where this species was collected.

Type material. HOLOTYPE, large preparatory female, body length (bl) 8.2 mm, not dissected, left uropod missing one ramus. Australian Museum catalogue number (AM) P40752.

PARATYPES. Illustrated and/or dissected specimens: copulatory male, bl 6.7 mm (P40753); copulatory male, bl 6.1 mm (P40754); copulatory male, bl 7.4 mm (P40755); brooding female, bl 7.0 mm (P40756); preparatory female, bl 6.0 mm (P40757); brooding female, bl 6.5 mm (P40758); 29 specimens, AM P40759, 5 specimens AM P38513. PARATYPE female, deposited at Northern Territory Museum, Darwin (from AM P38513). PARATYPE female deposited at Museum of Victoria, Melbourne, registration number J23755 (from AM P40759).

Type locality. WFP Station K1 (see Fig.14). Small unnamed spring, north-east side of Oscar Range, Kimberley Region, West Australia. Collected by WFP, 30 June 1988. 4.3 km north-west of Elimberrie Spring, 17°39'S 125°01'E (Leopold Downs, 1:100,000 series, 136477). A small spring flowing as a narrow trickle into a small, slow flowing stream up to about 1 m wide. Slope about 2°. Water depth 1-2 cm, clear, pH about 7.8, conductivity 560, water temp. 26°C (air temp. 30°C). Filamentous green algae and roots. Substrate limestone boulders on mud and silt. In small gully with rain forest trees and shrubs. Some cattle damage. [Ellaway *et al.* (1990) give the following data for 9 May 1988 for what is assumed to be the same spring (their station 5):- temp. 27°C (air 31.5°C), pH 7.27, conductivity 460].

Habitat. Washed from algae and/or roots at spring head.

Distribution. Known only from type locality, an unnamed spring near the northern end of the Oscar Ranges.

Diagnosis. Pleotelson rounded distally with distinct gap between distal 2 major sensillate setae. Endopod of female pleopod I length 0.57 exopod length. Outer lobes of maxilla with 7 comb setae (each seta with row of regular flattened denticles).

Description. Body lengths as follows: brooding females 6.5-7.0 mm; preparatory females 5.7-8.3 mm, early preparatory female 5.1 mm; juvenile females 46.0-65.5 mm; copulatory males 6.1-7.4 mm; precopulatory male 4.4 mm; juvenile males 47.0-54.5 mm; mancas 33.5-35.5 mm.

Head (Fig.2C,E) freely articulating with pereonite 1, with presumed (blind) eyelobes lateral to insertion of antennae. Length 0.82 width; head dorsal surface length 1.5-1.7 first pereonite medial length. Anterior margin medially concave, with anterolateral flattened

projections covering insertions of antennae. Dorsal surface oval, covered with scattered fine setae, demarcated from lateral surface by thin cuticular ridge. Antennular insertions closely spaced medially. Interantennular ridge narrow, terminating ventrally in rounded frontal projection vertically adjacent to clypeus. Clypeus rounded, nearly as broad as space including antennal insertions, with narrow socket for mandibular articulation. Labrum distally rounded, setose on anterior and ventral sides, only slightly asymmetrical.

Pereon (Fig.1). Total body length 4.8-6.1 width measured at pereonite 3. Medial length 0.41 body length. Pereonite 1 laterally longer than subequal pereonites 2-7. Pereonite 7 shorter than proceeding segments. Dorsal surfaces of each segment with 2 transverse rows of simple setae, just behind anterior segment and at posterior margin; tiny hair-like setae most dense at lateral margins. Dorsal surfaces of each segment with 1 or 2 thin transverse cuticular ridges.

Pleon (Figs 1,3A,D). All segments articulated flexibly, having ability to rotate in both vertical and transverse axes; pleotelson especially free in transverse axis with possible rotations approaching 90° driven by strong muscles in pleonite 5. Medial length 0.43 body length. Segments increasing in medial length posteriorly; pleonites 1-5 medial length - pleon length ratios: 0.11, 0.11, 0.13, 0.13, 0.22. Pleotelson medial length 0.39 pleon length; length 0.97 width. Dorsal setal distributions on free pleonites similar to that of pereon, with 2 rows of larger simple setae on each segment. Pleotelson with scattered dorsal simple setae, posterolateral margins with 6 larger, more robust sensillate setae and 16 small simple (nonsensillate)

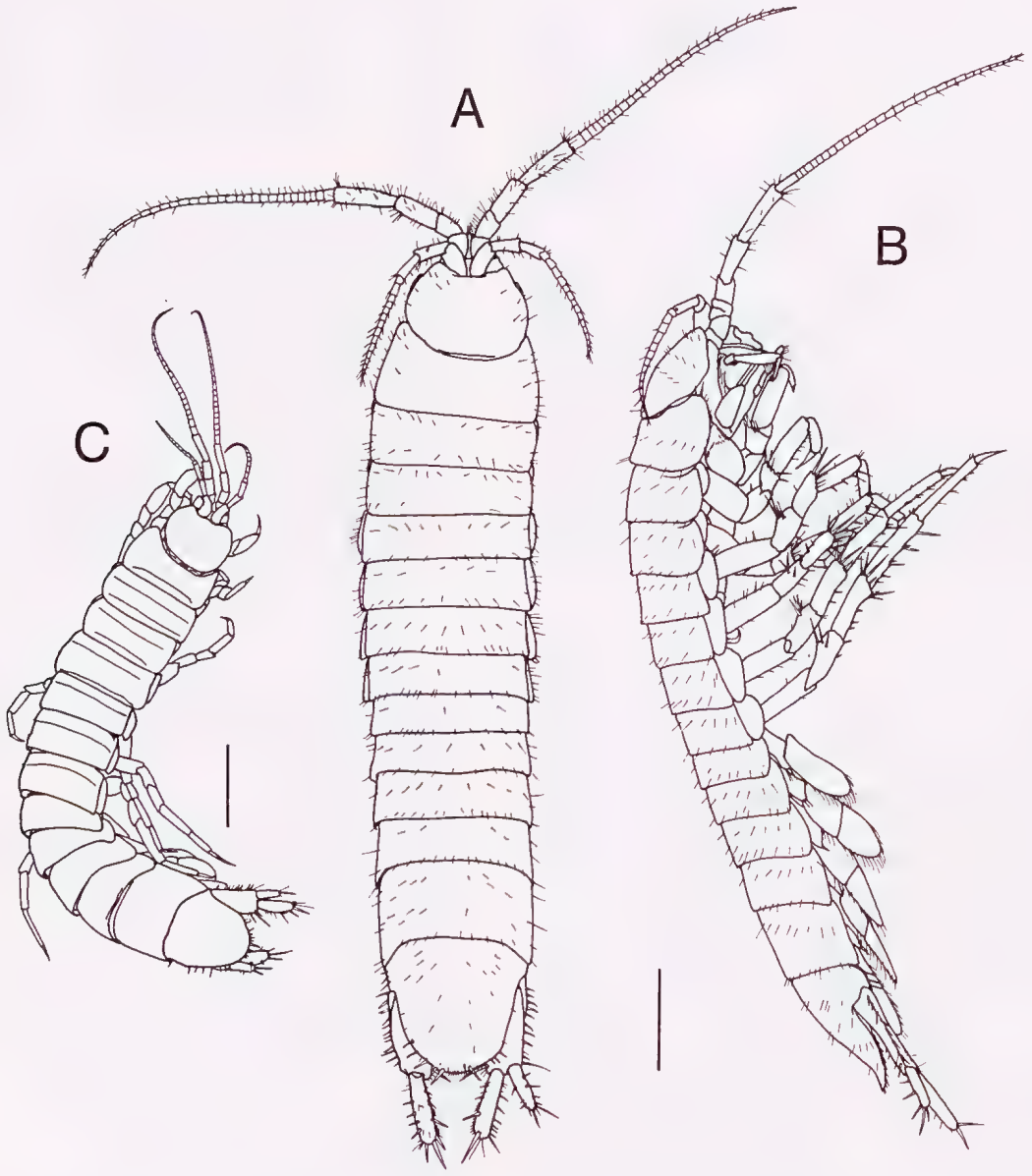

Fig.1. *Tainisopus fontinalis* n.gen., n.sp. A-B, holotype preparatory female, Australian Museum catalogue number (AM) P40752, dorsal and lateral views. C, paratype copulatory male, AM P40755, dorsal view. Scale bars = 1 mm.

tooth-like setae: 2 largest terminal sensillate setae separated by distinct space occupied by only small simple tooth-like setae. Pleon lacking dorsal transverse ridges.

Antennula (Figs 1,2A-C) not sexually dimorphic, curving laterally and posteriorly in most specimens. Length 0.22-0.24 body length, with 16-18 articles in adults. Article 1 strongly curved laterally, with few simple setae, and with cuticular scales on medial margin. Articles 2-3 shorter than article 1, decreasing in length distally. Article 3 lacking penicillate setae. Well-defined remnant of second flagellum on anteromedial margin of article 3, with several large setae and at least 1 penicillate seta. Basal flagellar article 4 with penicillate setae, shorter than either protopodal article 3 or main flagellar article 5. More distal articles having simple setae and aesthetascs on distal margins. No more than 2 aesthetascs on each article with most having only 1, proximal and distal articles lacking aesthetascs. Aesthetascs consisting of narrow proximal peduncle, enlarged thin distal part, and distal tip with tiny pore.

Antenna (Figs 1,2C-D). Length 0.57 body length, with 31-38 articles in adults. Articles 1-3 subequal, with few simple setae, but with many cuticular combs and scales. Article 3 with tiny circular scale surrounded by articular membrane, adjacent to papillose structure. Article 4-6 longer than basal articles, increasing in length distally. Flagellum length 0.6 total antenna length.

Mandibles (Fig.4). Body of mandible robust and

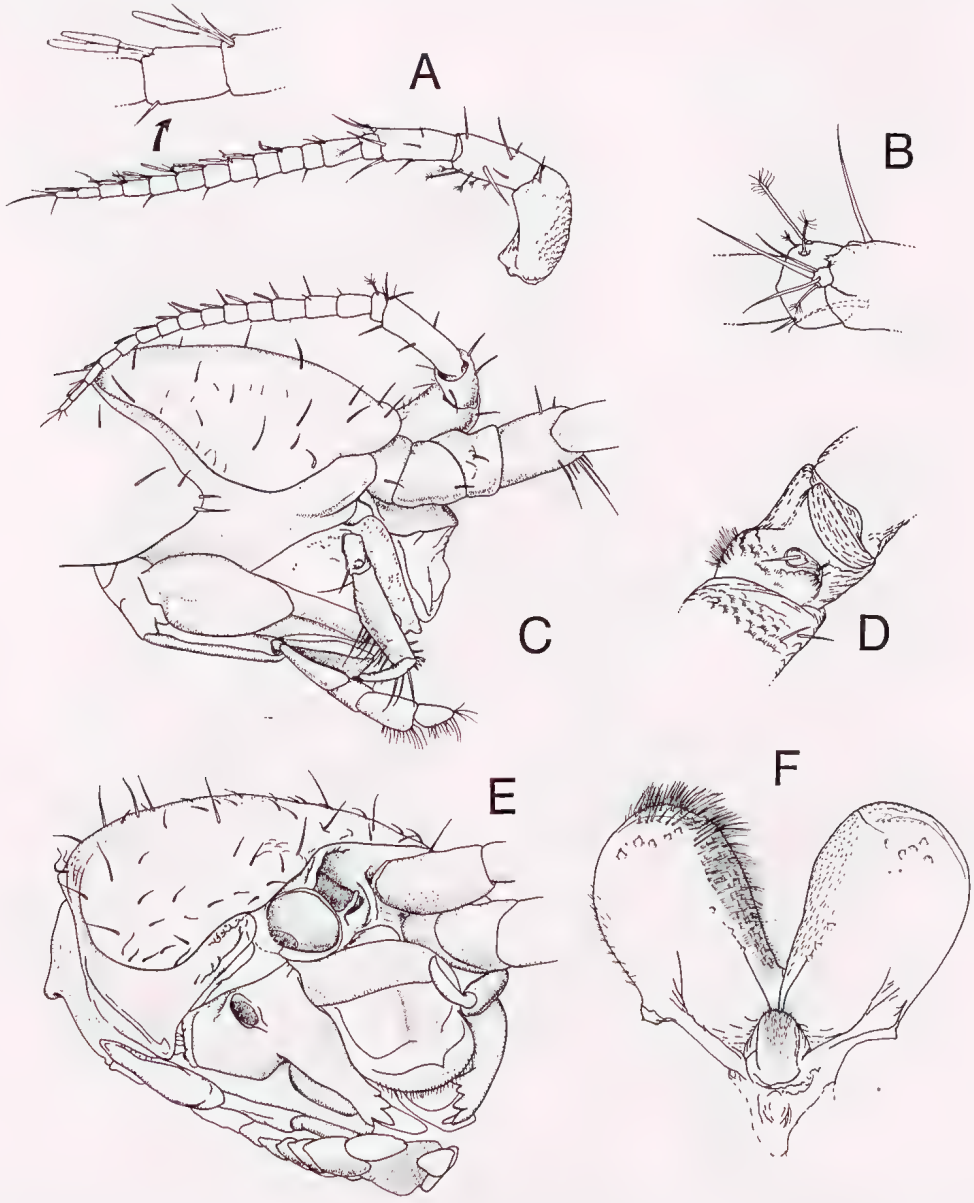

Fig.2. *Tainisopus fontinalis* n.gen., n.sp. A, left antennula, dorsal view. B, left antennula, enlargement of accessory flagellum on article 3. C, lateral view of intact head. D, antenna, enlargement of article 3 showing reduced antennal scale. E, frontal oblique view of head, antennula, antenna and mandibular palp removed. F, paragnaths, ventral view, setae omitted on left side. A-B, D-E from copulatory male, AM P40753; C from holotype female, AM P40752; F from paratype female, AM P40757.

broad; articular axis (defined by line between dorsal condyle and posterior extension of mandible) at approximately right angles to incisor process. Incisor processes with 4 teeth, with second tooth from ventral side largest and most projecting; 2 dorsal teeth shortest and more rounded. Left lacinia robust, somewhat flattened and curved, with 3 teeth. Right lacinia resembling modified and fused members of spine row but with broad rounded base and 4 denticulate terminal subspines curling in posteromedial direction. Spine row with 6 denticulate members on right side and 7 on left; posteriormost spine smaller than more anterior members and on left side distinctly set apart from more distal row members. Molar process short, broad, distal margin on dorsal and posterior with many small denticles and many fine setae; distal triturating surface flat, irregularly granular or denticulate. Dorsal condyle rounded, hook-like, articulating with head in rounded socket on lateral edge of clypeus. Palp approximately same length as body of mandible; articles 2-3 with many denticulate or setulate setae on distal ends and cuticular combs covering opposing surfaces; article 3 only slightly curved, projecting laterally at right angle from article 2.

Maxillula (Fig.5A,B). Outer lobe with 12 robust setae: 5 medial setae with strong posteromedial directed teeth. Inner lobe with 4 large densely setulate setae and 2 small simple setae. Inner and outer margins of both

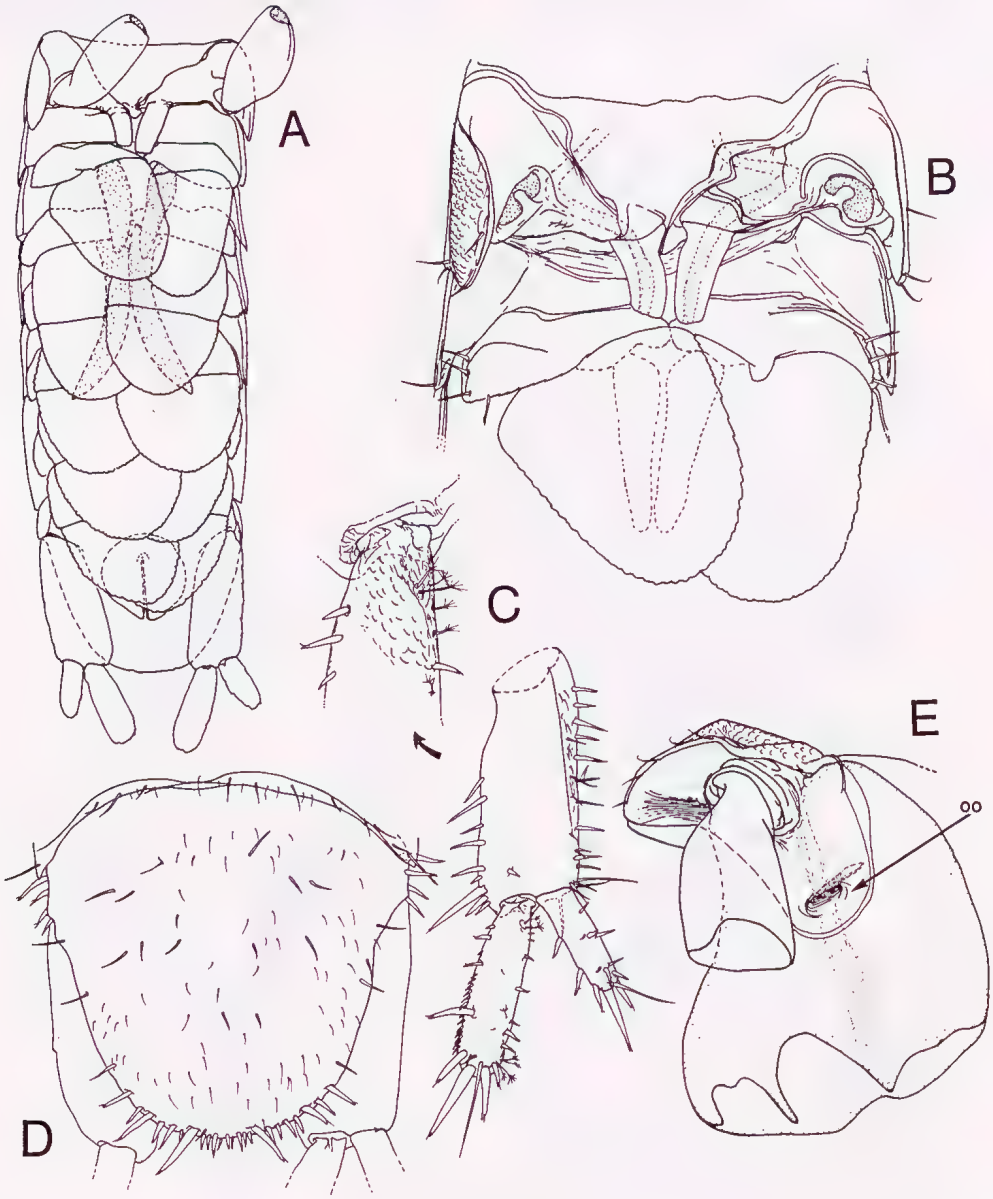

Fig.3. *Tainisopus fontinalis* n.gen., n.sp. A, ventral view of posterior pereon, pleonites and pleotelson showing form of penile papillae and pleopod arrangement. B, enlargement of genital area from A. C, right uropod and enlargement of basal area of uropodal protopod (upper left), dorsal view, drawn *in situ*. D, pleotelson, dorsal view, detail of uropods omitted. E, posteroventral oblique view of pereonite 5 and oostegite, brooding female, medial part of coxa seen through oostegite, showing medial position of oopore (indicated by arrow and **oo**), pereopod V truncated. A-B from paratype male, AM P40754; C-D from holotype female, AM P40752; E from paratype brooding female, AM P40756.

lobes with fine hair-like setae.

Maxilla (Fig.5C). Lobes short and robust. Inner lobe distal and medial surface densely covered with setulate and spinulate setae: 3 large medial setulate setae; 13 outer more distal setae in 2 rows (5 in ventral row, 8 in dorsal row) with both spinules and setules.

Maxilliped (Fig.5D,E). Basis elongate and narrow, width at either base of palp or at endite 0.2 length. Endite with 4 coupling hooks; distal tip with 9-11 robust radially plumose setae, 3-4 subdistal smooth setae, and 1 squat lightly setulate seta on medial corner. Dorsal longitudinal ridge of basal endite with 6 setulate setae, and with extremely fine, hair-like setae along proximal section, especially below palp. Palp wider than endite, palp article 3 width 1.3 basis width. Palp articles 3 and 4 with 18-27 and 14-24 simple setae, respectively. Palp article 5 with 17-25 simple setae, single most distal seta with single row of setules. Epipod broad, rounded, width 0.78 length, with cuticular combs on ventroproximal surface and on lateral margin; distomedial margin with extremely fine, hair-like setae.

Pereopod I (Fig.6A). Length 0.22-0.32 body length, not sexually dimorphic, distinctly subchelate with major hinge between propodus and dactylus. Dactylus distal tip with 1 primary claw and tiny denticulate accessory claw, separated by elongate, stiff sensillum and simple seta. Propodus robust and broad, much longer than carpus, with 9-10 robust bidenticulate sensillate setae. Carpus short, triangular with 3-4 robust bidenticulate sensillate setae. Merus short, trapezoidal with 3 robust bidenticulate sensillate setae on ventral side, and 6 elongate bisetulate setae on dorsal side. Basis approximately as long as ischium, merus, and carpus combined, with lateral flange and elongate

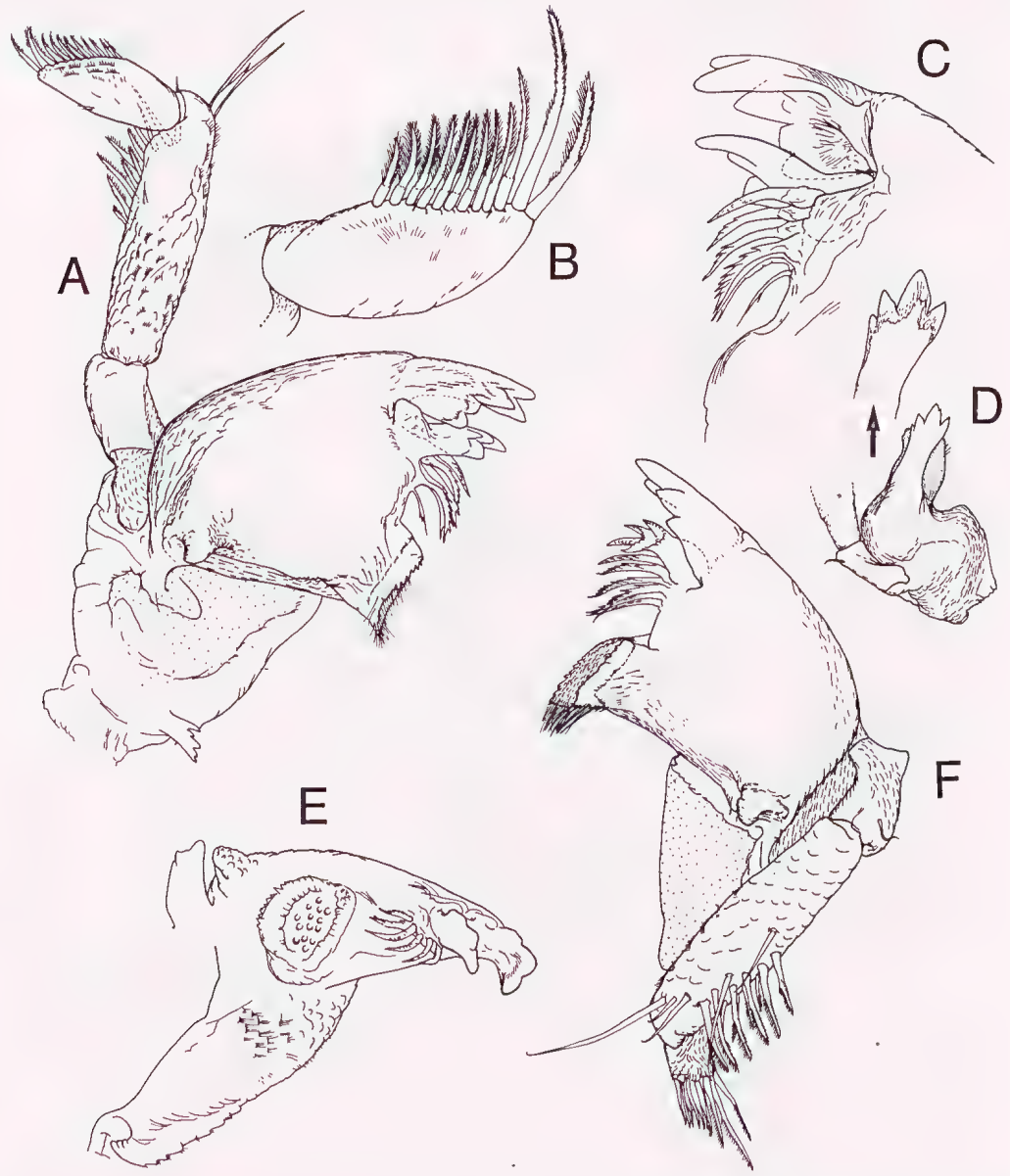

Fig.4. *Tainisopus fontinalis* n.gen., n.sp. Mandibles from paratype female, AM P40757. A, left mandible, dorsal view. B, right palp article 3, anterior view. C, left incisor process, lacinia mobilis and spine row, ventral view. D, right mandible, anterior view with enlargement of incisor process. E, left mandible, medial view, palp omitted. F, right mandible, dorsal view.

depression on anterior face for retraction of distal parts of limb. Coxa completely fused to pereonite 1 in both sexes.

Pereopods II-III (Fig.6B-D). Lengths 0.28-0.35, 0.29-0.36 body length, respectively. Not sexually dimorphic, moderately subchelate with major hinge between carpus and propodus. Dactylar distal tips each with one primary claw and tiny denticulate accessory claw, separated by elongate, stiff sensillum and simple seta; subdistal medial side of dactyli with 3 sensilla. Propodus elongate but shorter than carpus, with 2-4 small denticulate sensillate setae on ventral margin. Carpus robust and elongate, with approximately 16 robust bidenticulate sensillate setae on ventral margin. Merus with dorsal triangular projection bearing row of 4-5 elongate setulate setae. Basis with lateral flange and elongate depression on anterior face for retraction of distal parts of limb. Coxa of pereopod II completely fused to tergite 2; coxa of pereopod III ventrally fused to tergite 3, dorsally with distinct line of articulation, approximately half width of tergite.

Pereopod IV (Fig.7A). Ambulatory, not prehensile or subchelate, length 0.27-0.36 body length. Dactylar distal tip with primary claw, small dentulate accessory claw and single thick sensillum; subdistal medial side of dactylus with 3 sensilla. Carpus and propodus elongate, not robust, with 3-4 and 9 sensillate setae on medial margins, respectively. Ischium and merus with group of elongate sensillate setae on distodorsal projections. Basis with lateral-facing groove for retraction of ischium and merus. Coxa nearly as broad as tergite, with free tergal articulation and distinct lateral projection or plate.

Pereopod V-VII (Fig.7B-D). Broadly similar to pereopod VI, but increasing in length posteriorly: lengths 0.29-0.36, 0.0.33-0.43, 0.37-0.49 body length, respectively. Dactylar distal tip with primary claw, small dentulate accessory claw and single thick sensillum; subdistal medial side of dactyli with 3 sensilla. Carpi and propodi elongate, not robust, with 3-8 and 12-14 sensillate setae on medial margins, respectively.

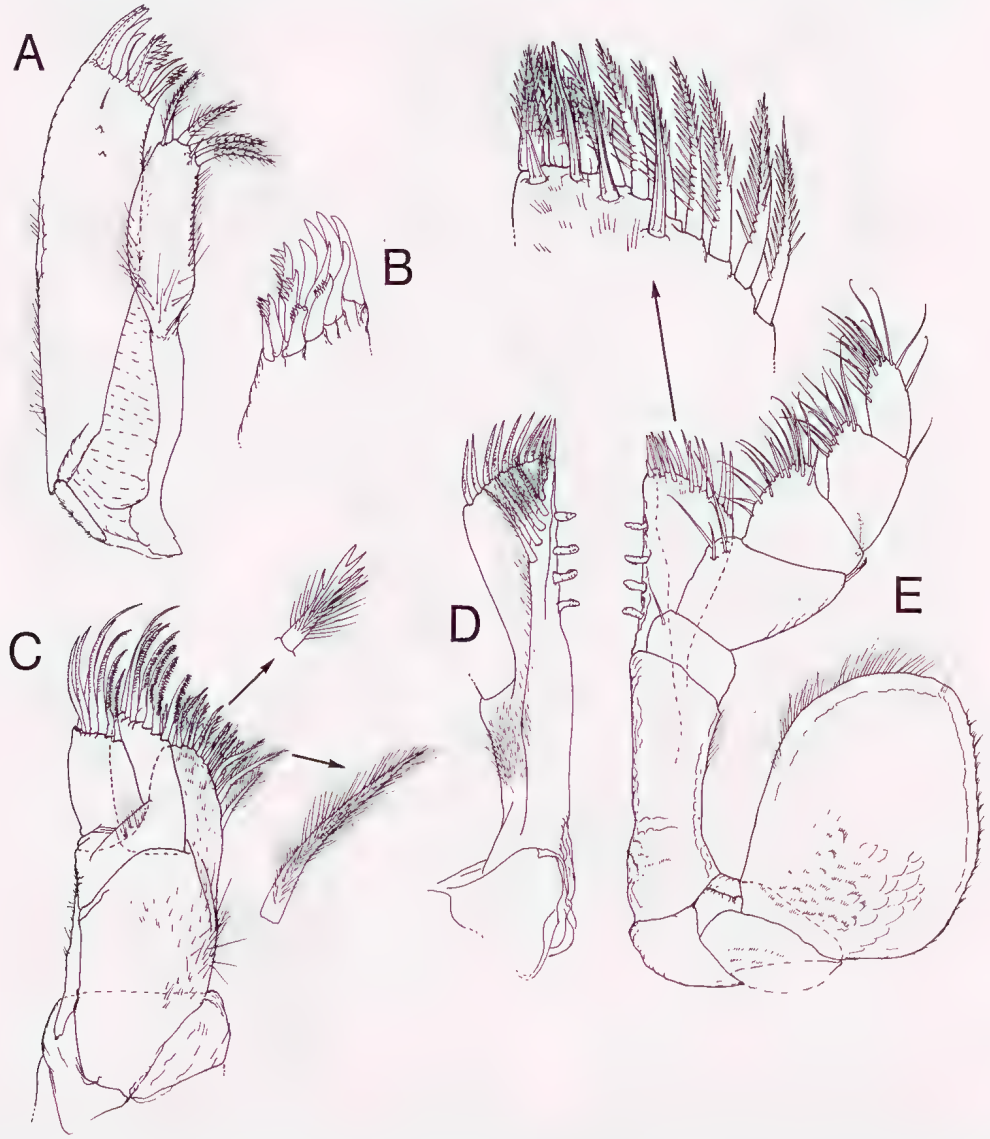

Fig.5. *Tainisopus fontinalis* n.gen., n.sp. Mouthparts from paratype female, AM P40757. A-B, right maxillula, dorsal view of whole limb and enlarged medial view of outer lobe. C, right maxilla with enlargements of setae from inner lobe. D-E, left maxilliped, dorsal view of endite and ventral view.

Ischium and merus with group of elongate sensillate setae on distodorsal projections. Basis with shallow posterior-facing groove for partial retraction of ischium and merus. Coxa as broad as tergite, with free tergal articulation and with distinct lateral projection or plate.

Pleopods (Fig.8). All similar in size and shape, covering entire ventral surface of pleotelson when retracted. Length/body length ratios: 0.10-0.12, 0.13-0.15, 0.14-0.16, 0.15-0.17, 0.13-0.15, respectively, females with proportionately longer pleopods. Protopods of pleopods I-V with broad insertions, expanded lateral plates bearing 3-6, 9-10, 9-13, 12-14, 13-18 elongate distally setulate sensillate setae, respectively. Protopods with medial projections bearing 2-3 robust setae with distal hooked tip and row of setules, overlapping with counterparts on opposite side (coupling setae). Exopods broad, covering smaller endopods, with distinct cuticular scales or sculpturing on anterior (or ventral) surface. Exopods of pleopods I-V with fringe of 31-40, 36-50, 40-60, 43-60, 40-56 biplumose setae, respectively; proximolaterally inserted setae shorter and with fewer setules than distally and medially inserted setae. Exopod of pleopod I of both sexes lacking division between proximal and distal segments; suture line only on anterior (or ventral) face in pleopods II-V. All exopods with medial ridge following medial margin approximately two thirds length so that cross section of exopod resembling flattened wedge with deepest part medially. Endopods of pleopods I-II various depending on sex. Endopod of male pleopod I simple, flattened, narrow, elongate, length 0.71 exopod length, widest just distal to narrow insertion, with single

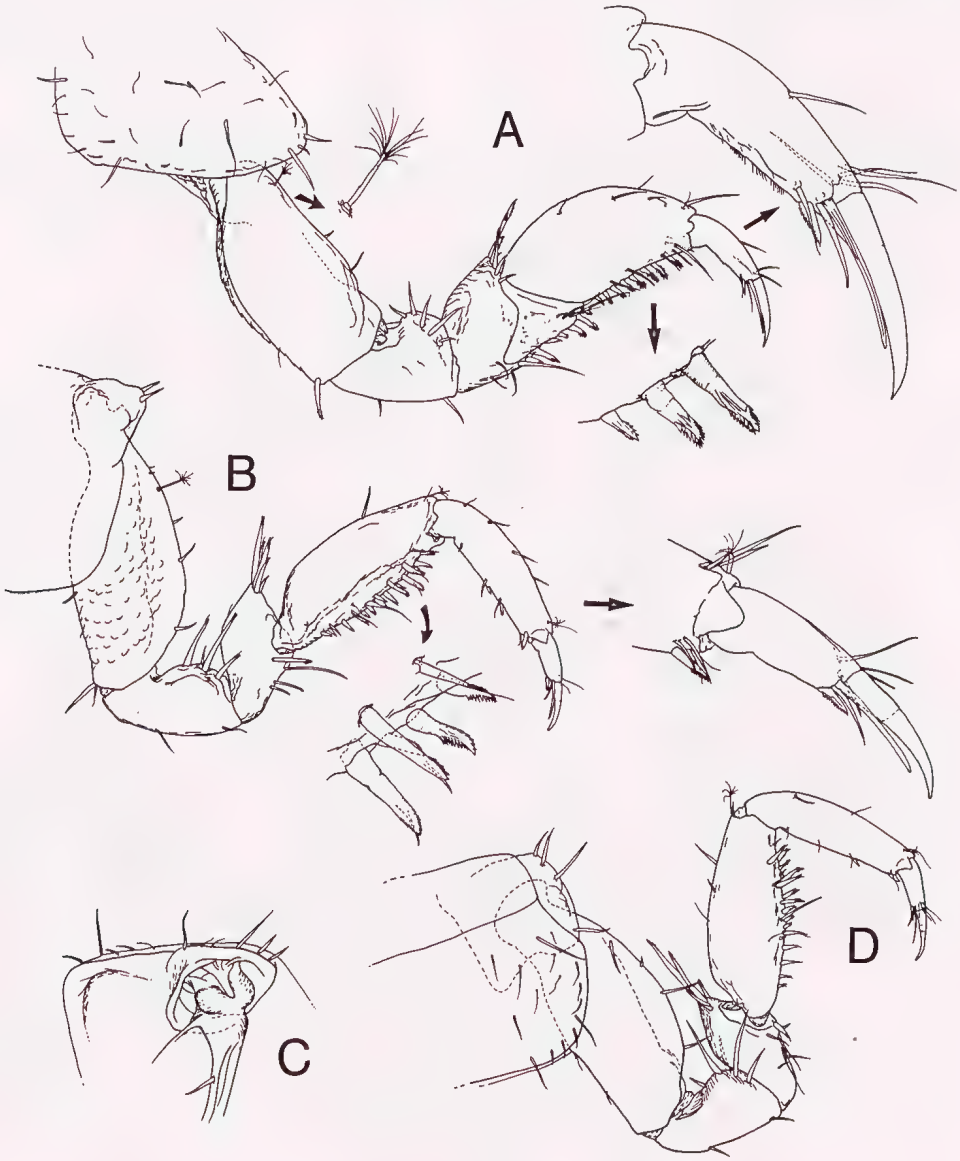

Fig.6. *Tainisopus fontinalis* n.gen., n.sp. Right pereopods I-III from paratype male, AM P40753. A, pereopod I, with enlargements of dactylus and proximal end of setal row on propodus. B, pereopod II, with enlargements of dactylus and distal end of setal row on carpus. C-D, ventrolateral view of coxa of pereopod III and lateral view of pereopod III.

distal biplumose seta and cuticular hairs on medial and distolateral margin. Endopod of female pleopod I similar with single distal plumose seta, but shorter, length 0.59 exopod length. Endopod of male pleopod II elongate, length subequal to exopod length, medioventral margin of distal tip with denticulate ridge and distomedial margin with minute cuticular hairs. Male endopods of pleopods III-V and female endopods of pleopods II-V similar: inserting approximately midway between exopodal insertion and medial margin, expanding into 3 distinct lamellae approximately 0.4-0.6 length of exopod; dorsal and ventral lamellae simple and flat; middle lamella thicker, folded into roughly transverse curved ridges, highest density of folding proximally.

Uropods (Figs 1,3A,C). Length 0.41-0.45 pleon medial length. Protopod longer than broad, approximately wedge shaped in cross-section with deepest part on lateral side, sensillate setae on both medial and lateral margins. Exopod shorter than endopod, length 0.48 protopod length, with sensillate setae distally and on margins. Endopod approximately oval in cross section, length 0.78 protopod length, with several different setal types: medial margin with proximal and distal groups of penicillate setae, all margins with sensillate setae becoming large distally, medial margin with row of 8-15 small tooth-like simple setae; distal tip with thin elongate simple setae.

Remarks. Much of the variation in the proportional lengths of various body parts is caused by variation in the body length. Compared to some specimens, the holotype female is axially compressed. If a length-width ratio of another individual is multiplied by the holotype's width, its length could be near 10 mm, rather than 8.2 mm. This disparity suggests that both the width

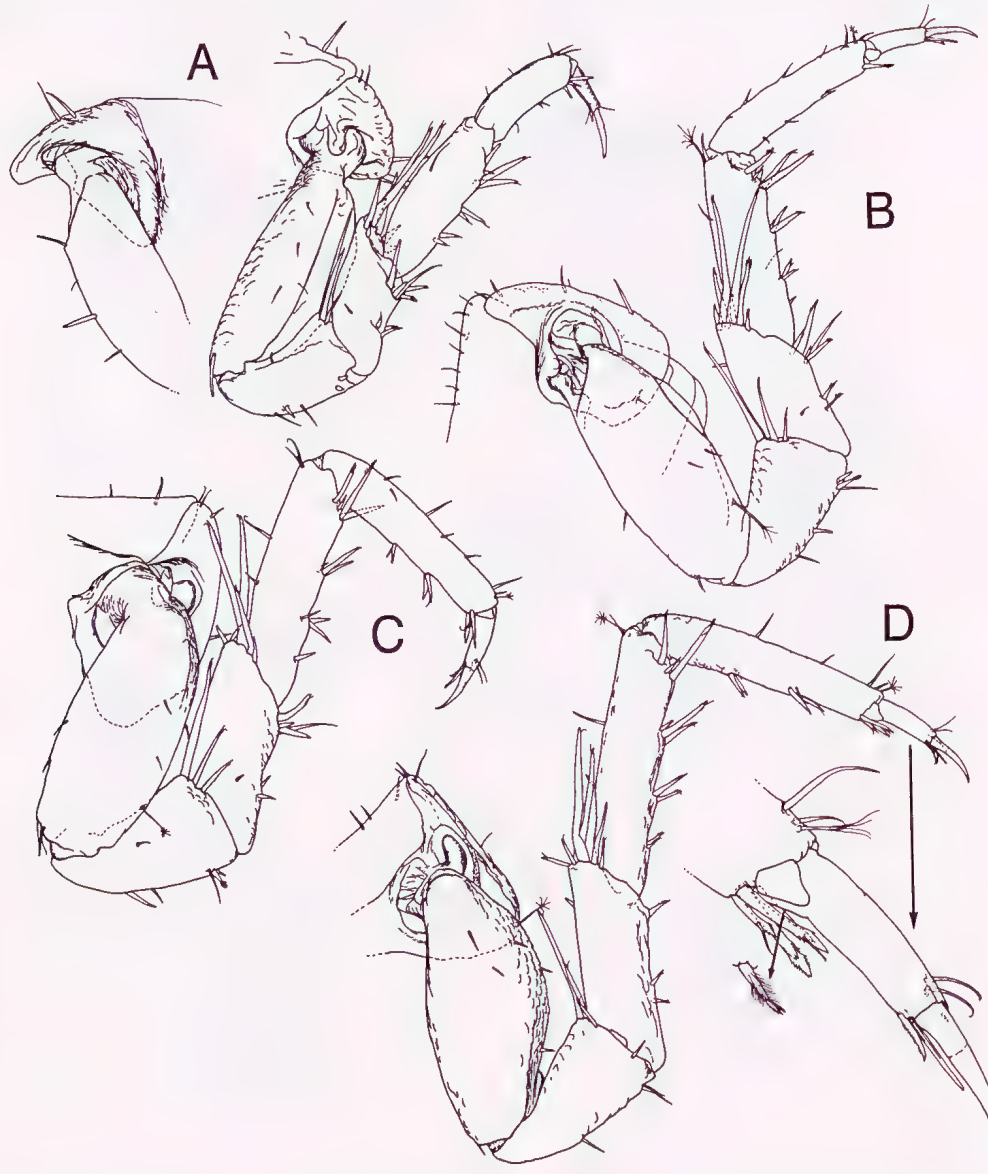

Fig.7. *Tainisopus fontinalis* n.gen., n.sp. A-D, right pereopods IV-VII, in lateral view but rotated anteriorly, from paratype male, AM P40753. A, pereopod VI including anterior view of coxa. D, pereopod VII with enlargement of dactylus.

and the length contain significant individual or preservation-dependent variation. Consequently, ratios using body length cannot be diagnostic. Variation in the body segments appears to be a function of the relative compression or expansion of both the pereon and pleon, which may be a function of preservation. The holotype was chosen because it seemed the most undamaged by preservation. Despite this apparent variation due to preservation or other sources, the lengths of these specimens compared to their developmental states show consistent patterns (see "Population Biology" below).

Tainisopus napierensis n.sp.

Figs 9-12

Etymology. *Tainisopus napierensis* refers to the Napier Range where this species was collected.

Type material. HOLOTYPE. Large preparatory female, body length 8.35 mm, appendages dissected off right side after intact specimen illustrations were made. AM P40760. No other specimens available.

Type locality. WFP Station K10 (see Fig.14). Outer pool of Napier Downs Cave (= Old Napier Cave or local name Lake Cave), Napier Ranges, Kimberley Region, West Australia. Collected by WFP, 3 July 1988, 17°14'S 124°38'E (Lennard, 1:100,000 series, 745945). Flood prone, still pool in outer part of cave with some roots. Water depth up to 1 m, clear, pH about 7.66, conductivity 260, water temp. 20°C. Substrate limestone rock, some boulders with gravel, sand, mud and silt. Atyiid shrimps common. [Ellaway *et al.* (1990) give the following data for 9 May 1988 for what is assumed to be the same pool:- temp. 26.5°C (air 31.5°C), pH 7.93, conductivity 273].

Habitat. The specimen was caught with a net in the pool where it was swimming with atyiid shrimps.

Distribution. Known only from the type locality.

Diagnosis. Pleotelson obtusely pointed distally without large gap between distal two major sensillate setae. Endopod of female pleopod I length 0.28 exopod length. Outer lobes of maxilla with 9 comb setae.

Description of holotype female, differences from *T. fontinalis*. *Body features* (Figs 9, 11C). Body

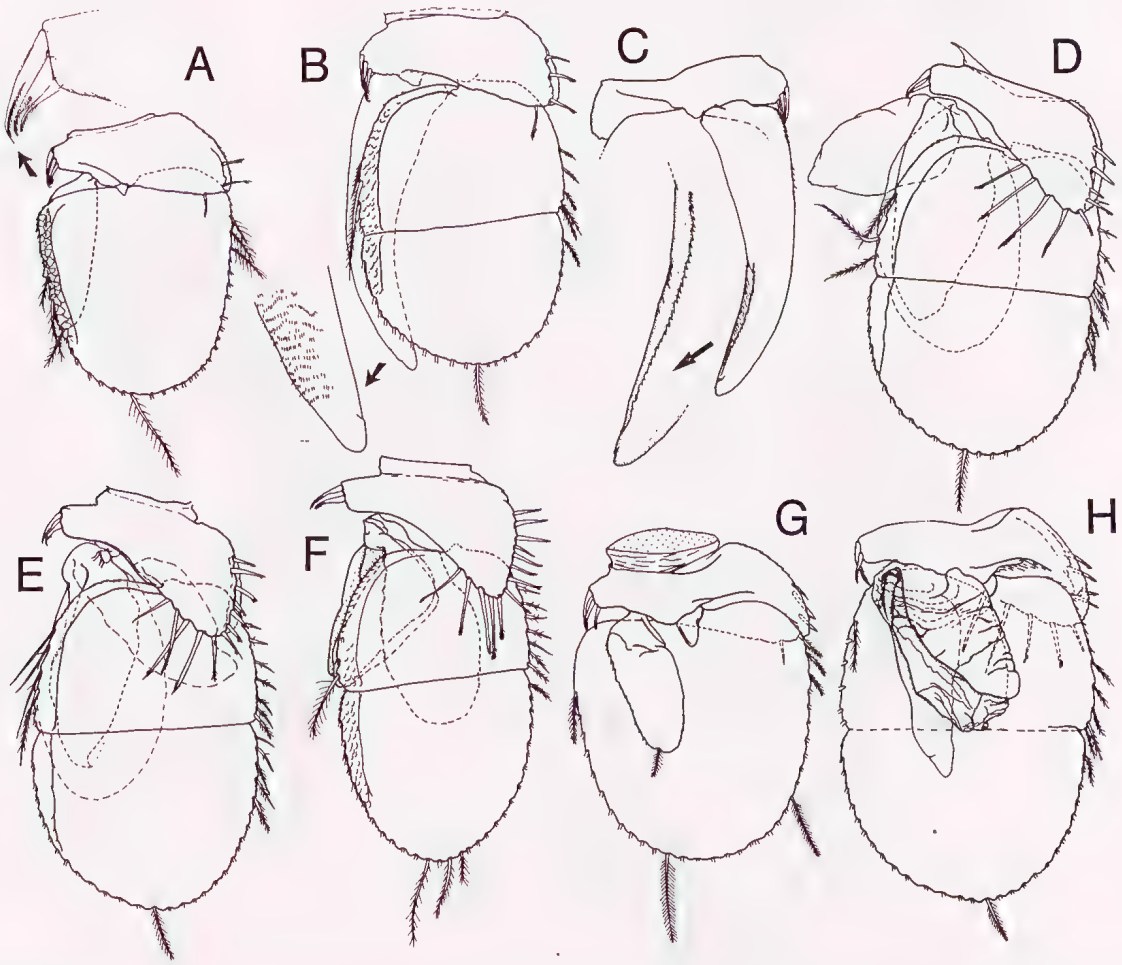

Fig.8. *Tainisopus fontinalis* n.gen., n.sp. A-F, left pleopods I-V from paratype male, AM P40753. A, pleopod I with enlargement of medial coupling setae. B, pleopod II, with enlargement of endopod distal tip, ventral view. C, endopod of pleopod II, with enlargement of distal tip, dorsal view. G-H, left pleopods I-II, dorsal view, from brooding female, AM P40758.

length 5.2 width measured at pereonite 3. Head length 0.85 width. Pereon medial length 0.43 body length. Pleon medial length 0.45 body length. Pleonites 1-5 medial length - pleon length ratios: 0.10, 0.10, 0.14, 0.12, 0.19. Pleotelson medial length 0.36 pleon length; pleotelson length 1.03 width. Pleotelson tip with 7 large sensillate setae and 13 small nonsensillate setae (using bilateral symmetry as a guide, the odd numbers suggest that an average specimen of same size may have 8 large and 12 small, or 6 large and 14 small setae).

Antennula (Fig.9) Length 0.25 body length, with 18-19 articles.

Antenna (Fig.9). Length 0.55 body length, with 36-38 articles. Flagellum length 0.57 total antenna length.

Mandibles. Spine row with 5 denticulate members on right side, 6 on left.

Maxilla (Fig.10A). Inner lobe with 3 large medial radially setulate setae; 18 more distal setae in 2 rows (7 in ventral row, 11 in dorsal row) with both spinules and radially arranged setules.

Maxilliped (Fig.10B). Basis width at either base of palp or at endite 0.22 length. Endite distal tip with 13 robust radially plumose setae, 4 subdistal smooth setae, and 1 squat lightly setulate seta on medial corner. Dorsal longitudinal ridge of basal endite with 5 radially setulate setae. Palp articles 3-5 with 44, 34, 25 medial simple setae, respectively. Epipod width 0.81 length.

Pereopods (Figs 9B,11A). Propodal and carpal

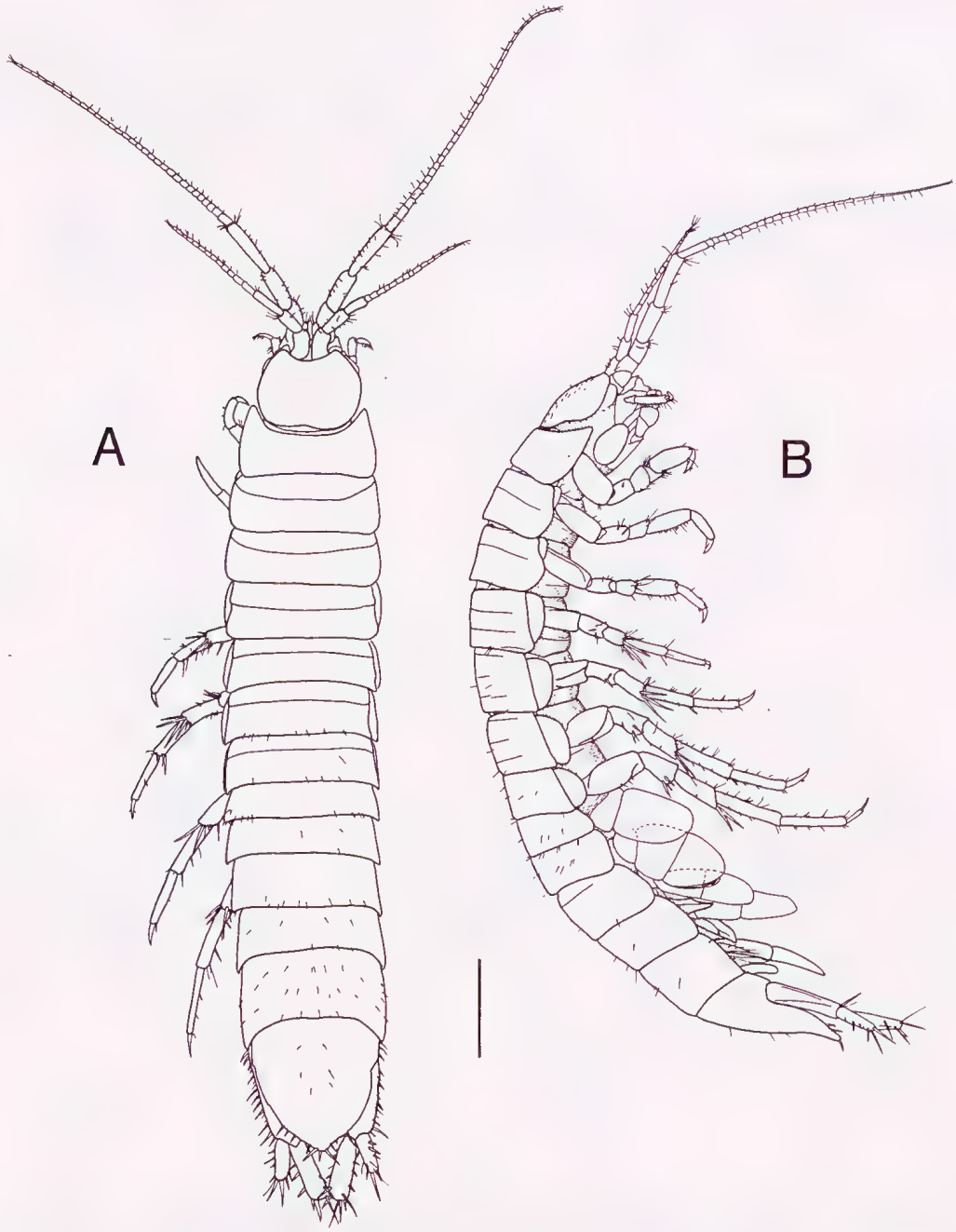

Fig.9. *Tainisopus napierensis* n.sp. Holotype, AM P40760. A-B, dorsal and lateral views. Scale bar = 1 mm.

ventral margins of pereopod I with 11 and 4 robust bidenticulate sensillate setae, respectively. Carpus of pereopods II-VII with 18, 18, 13, 15, 17, 16 robust bidenticulate sensillate setae on ventral margin, respectively.

Pleopods (Fig.12). Flattened lateral plate of protopods I-V with 6, 11, 11, 14, 18 distally setulate sensillate setae, respectively. Exopods of pleopods I-V with 41, 50, 59, 64, 59 fringing biplumose setae, respectively.

Uropod (Fig.11B). Length 0.18 body length; length 0.40 medial pleon length. Exopod length 0.44 protopod length, with sensillate setae distally and on margins. Endopod length 0.80 protopod length; distomedial margin with 11 small tooth-like simple setae.

Remarks. *Tainisopus napierensis* is imperfectly described owing to the availability of only one specimen, the holotype. Although it is not described as fully as *T. fontinalis*, the holotype was fully dissected on one side and comparisons were made between the two species. We feel justified in erecting this new species because the features that differ between the two species are constant in *T. fontinalis*, indicating that these features are also likely to be relatively constant in *T. napierensis*. The species level distinctness of these two forms, however, should be considered a hypothesis to be tested by the recovery of additional material of both species.

Tainisopus napierensis is most easily identified by its subangular pleotelson tip with no obvious gap between the large terminal sensillate setae. Because the pleotelson form is reasonably constant in *T. fontinalis*, this species should also be consistent for this feature,

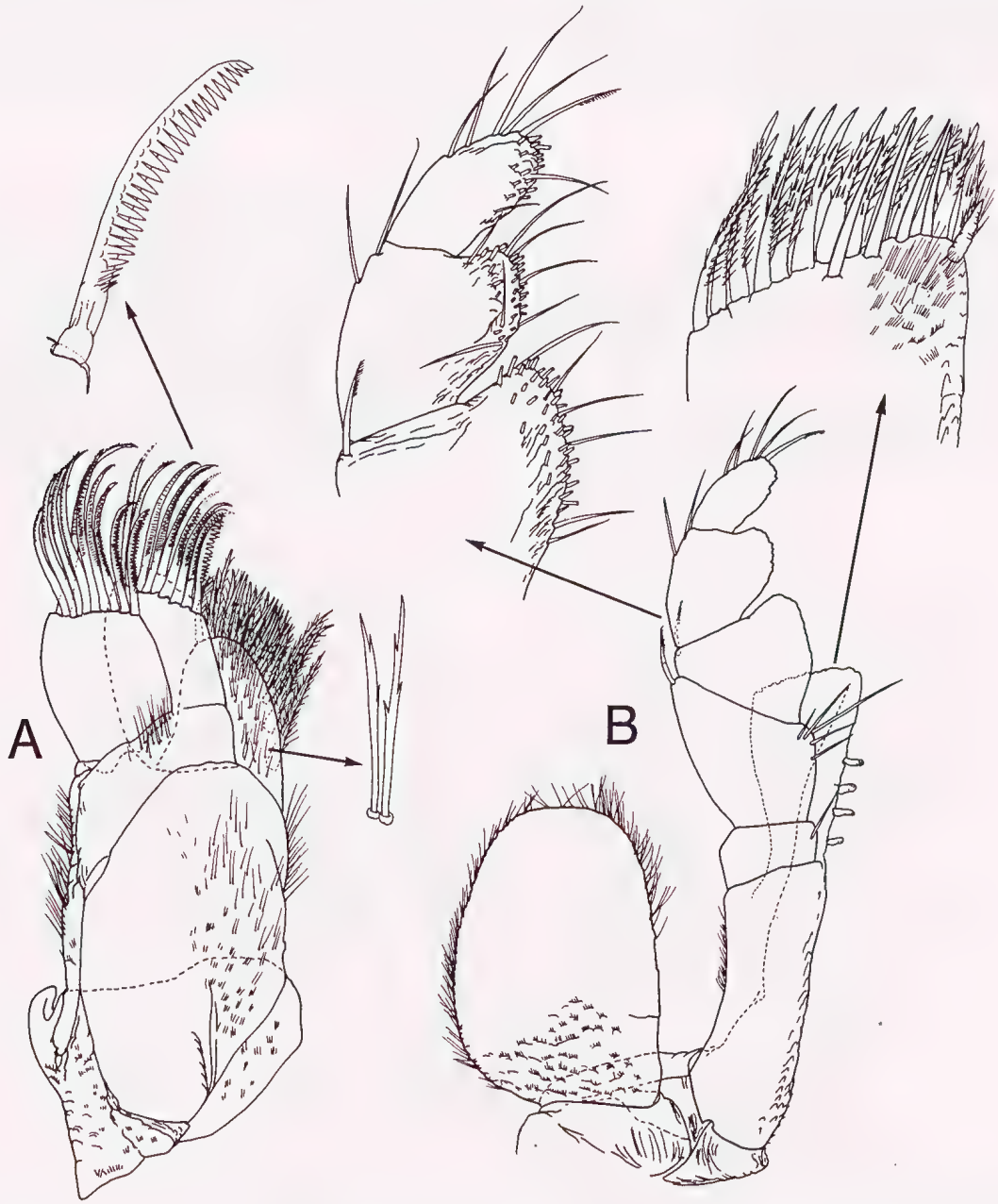

Fig.10. *Tainisopus napierensis* n.sp. Holotype, AM P40760. A, right maxilla with enlargement of comb seta from middle lobe and fine setae from inner lobe. B, right maxilliped, with enlargement of endite distal tip and setae on palp segments 3-5, most setae truncated.

assuming the species concept is correct. This hypothesis and it alternative (conspecific geographic variation in *T. fontinalis*) can be tested by the acquisition and study of variation in more specimens. The setal counts of the pereopods and pleopods are essentially identical to that of similar-sized specimens of *T. fontinalis*, suggesting at least a sister group relationship between the two species. Many ratios of measurements show small differences between the two species, although most are unlikely to be statistically significant. In *T. napierensis*, the maxillipeds have more large setae than in *T. fontinalis*, although the setal counts vary allometrically in the latter species. The number of comb setae on the outer lobes of maxillae, however, do not vary in adults of sizes of 6 to 9 mm in *T. fontinalis*; therefore, a count of nine comb setae on the outer maxillary lobes of *T. napierensis* appears to be a useful diagnostic character. The endopod of the female pleopod I in *T. fontinalis* is consistently larger than in *T. napierensis*, allowing this character to also be used in the diagnosis.

Tainisopus spp.

Material. Single damaged preparatory female, body length approximately 6.6 mm, missing most of pleotelson and one uropod, more anterior parts of body and pereopods intact from WFP station K2, AM P40779. Single intact female, WFP station K5.

Localities. WFP Station K2 (see Fig.14). Unnamed spring, north-east side of Oscar Range, Kimberley Region, WA. Collected by WFP, 30 June 1988. 1.2 km south-east of Elimberrie Spring, 17°40.08'S 125°03'E (Leopold Downs, 1:100,000 series, 179452). A small spring flowing as a small trickle into a slow flowing stream 0.5-1 m wide, 1-3cm deep. Slope about 5-10°. Clear, pH about 7.14, conductivity 500, water temp. 28.5°C (air temp. 31°C). No aquatic vegetation except some roots. Substrate limestone boulders on sand, mud and silt. Few trees and *Pandanus*. Some cattle damage.

WFP Station K5 (see Fig.14). Elimberrie Spring, north-east side of Oscar Range, Kimberleys Region, WA. Collected by WFP, 1 July 1988. 17°39.83'S, 125°02.5'E (Leopold Downs, 1:100,000 series, 179452). A small spring with its outlet pooled and fed to a tank by a pipe. The clear, still water in the pool at the head of the spring is about 10 cm deep. Clear, pH about 6.7, conductivity 550, water temp. 24°C (air temp. 29°C). No aquatic vegetation except some roots. Substrate limestone boulders and sand. Small trees provide a partial canopy.

Habitat. Washed from roots at spring head.

Distribution. Springs near the northern end of the Oscar Ranges.

Remarks. A single damaged female specimen, recovered from WFP station K2, is clearly unlike either *T. fontinalis* and *T. napierensis*. Because of the current uncertainty of its classification, this specimen is only provisionally assigned to *Tainisopus*. Furthermore, the generic description was not modified to account for this specimen, which differs in several important points. The pereopods are longer and less differentiated than in *T. fontinalis* and *T. napierensis* where the change between pereopod III to pereopod IV is substantial. This

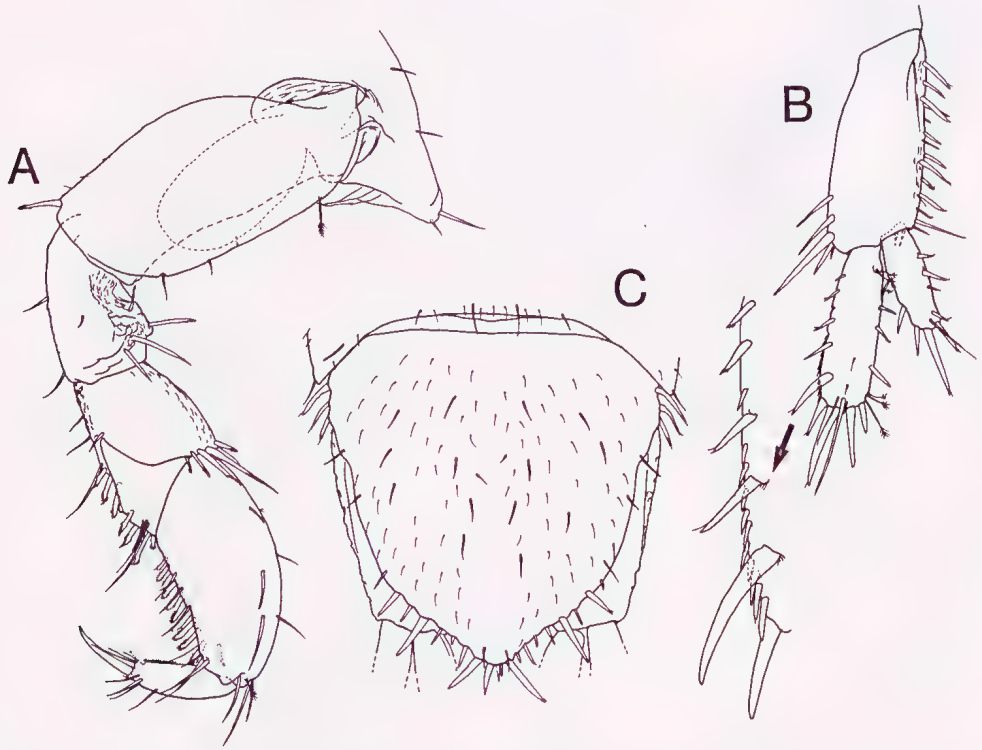

Fig.11. *Tainisopus napierensis* n.sp. Holotype, AM P40760. A, right pereopod I, lateral view. B, right uropod, with enlargement of setal rows on medial side of endopod. C, pleotelson, dorsal view.

specimen seems to lack the endopods of the pleopods, and instead has a thickened region of the medial part of the exopod. The uropods and pleotelson tip are also much more setose. A new genus-level taxon may be necessary to classify this specimen. Another specimen of *Tainisopus* from WFP station K5 was discovered after this paper was completed. It, too, appears to be a different species based on its setation, but is more similar to *T. fontinalis* and *T. napierensis*.

Discussion

Relationships. *Tainisopus* is unusual because it bears no apomorphies (that we recognise) that unquestionably ally this taxon with any of the established isopod suborders. Some possible hypotheses of classification within the existing subordinal system are as follows.

1. "*Tainisopus* is a derived phreatoicidean". Presumed synapomorphies driving this hypothesis are the enlarged pleonite 5, equality of the other pleonites and all pleopods, the general shape of the uropods, presence of multiple lobes on the pleopodal endopods (found in the hypsimetopine phreatoicideans). All other features not agreeing with known phreatoicideans are considered derived features within the suborder.

2. "*Tainisopus* is a member of the asellotan-microcerberid clade". Features central to this hypothesis are three distinct protopodal articles of the antenna, clear remnants of the antennal scale on article 3, and an arrangement of the male penes and coxae of pereopod VII similar to that found in possibly early-derived Asellota (Just & Poore, 1992). In the cladograms of Brusca & Wilson (1991), the antennal characters exhibit a reversal throughout the Peracarida, and become synapomorphies of the asellotan-microcerberidan clade.

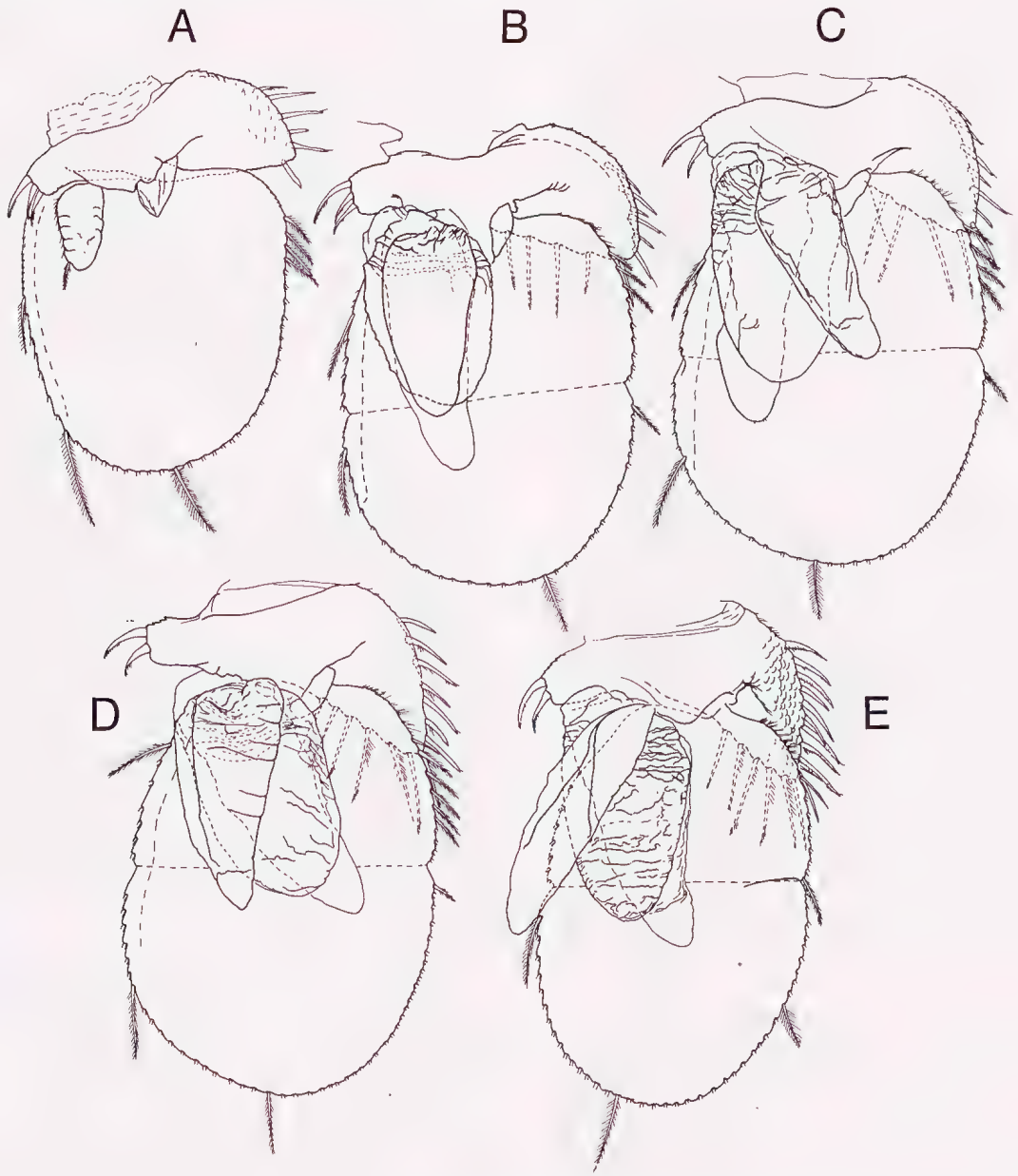

Fig.12. *Tainisopus napierensis* n.sp. Holotype, AM P40760. A-E, pleopods I-V, dorsal view.

If these features are interpreted as apomorphies, then they would argue for inclusion of *Tainisopus* into the same clade. This, however, is a fairly weak hypothesis and is included here to allow comparison with the potentially important morphologies.

Other possible hypotheses are more difficult to interpret because the relationships of the higher Isopoda are currently not well understood (Brusca & Wilson, 1991). Therefore, we shall primarily confine ourselves to addressing these two hypotheses on the basis of character analysis, rather than a more concrete cladistic treatment. The main point of our argument may be summarised with the statement "Neither hypothesis can be true because (i) supposedly derived characters of *Tainisopus* may be plesiomorphies or at least shared with other taxa at the ordinal level and (ii) *Tainisopus* shares synapomorphies with the higher isopods, not seen in the phreatoicideans and asellotes".

The enlarged pleonite 5 of *Tainisopus* has been regarded as a synapomorphy of the Phreatoicidea (Nicholls, 1943). Other taxa also have an enlarged pleonite 5: Limnoriidae, Lynseiidae, and Anthuridea (where the pleonites are distinctly separate). Other isopod groups may have an enlarged pleonite 5, although not as a frequent or defining trait. Many isopod taxa have subequal pleonites (where they are distinct), and this is the common state in all potential outgroups (Mictacea, Tanaidacea, Spelaeogriphacea). Consequently, this feature must be regarded as equivocal on relationships with the Phreatoicidea until a full reanalysis of the Isopoda is completed.

The "lacinia" on the right mandible (see Dahl & Hessler, 1982 for a detailed discussion of its derivation) could be a synapomorphy of the amphisopids and *Tainisopus*, because Nicholls (1943) felt this was a useful character to define the Amphisopidae. A right lacinia most similar to that of *Tainisopus*, however, is found in the Holognathidae (early derived Valvifera; see Brusca, 1984; Poore & Lew Ton, 1990). Lacinia-like spines on the right mandible are common among the Valvifera and Serolidae (G.C.B. Poore, personal communication). The typical phreatoicidean right lacinia is a flat toothed structure, rather different from the multispined right lacinia of *Tainisopus*. Moreover, the produced and often doubled spine row of the Phreatoicidea is unusual among the isopods (research in progress) and is quite unlike the more plesiomorphic morphology seen in *Tainisopus*. We conclude that the right lacinia is not a synapomorphy shared between the phreatoicideans and *Tainisopus*.

Multiple endopodal rami on pleopods III-V of *Tainisopus* may be a feature shared with some phreatoicideans, *Phreatoicoides* and *Hypsimetopus* in particular, although this is a variable feature in these taxa (Knott, 1975). Other isopods are also known to have multiple gill-like structures on the pleopods (Bathynomus, Bopyridae, Cymothoidae). The multiple rami could possibly be a special response to low oxygen tensions found deep subterranean waters but, more likely, an increase in pleopodal gill surface may be a response to increased activity and greater oxygen demand due to active swimming, not seen among the lower isopods, Asellota and Phreatoicidea. This feature seems equivocal for determining relationships, or may be an autapomorphy of *Tainisopus*.

The organisation of the pleotelson, although bearing some similarity between *Tainisopus* and phreatoicideans in the shape of the uropods, shows a substantial departure in morphoclines. *Tainisopus* has a broad and flat telsonic region (plesiomorphic, as in potential outgroups Mictacea or Spelaeogriphacea). The phreatoicidean pleotelson, however, is greatly modified for an amphipod-like pushing function, being vaulted and reflexed posteroventrally. If the *Tainisopus* pleotelson is in the same morphocline as the phreatoicidean pleotelson, then the *Tainisopus* form must be the earlier derived of the two. Associated with the pleotelson shape, the dorsoventrally flattened shape of the body is a standard feature of all isopods, and could easily be obtained directly from isopod ancestors, while the vaulted and elongate body form of the phreatoicideans is derived and not seen in any potential isopod outgroups.

A basal article in the antennal protopod is found in *Tainisopus*, Asellota and Microcerberidea. Although the analysis by Brusca & Wilson (1991) forces this feature to be a synapomorphy of the latter two taxa, this basal article may be an ancestral feature because it is also found in some Mysidacea. Authors have claimed that Amphipods and Cumacea have a three-articled protopod (e.g., Dahl & Hessler, 1982:134). Amphipods and Cumacea, however, lack a scaphocerite or scale to define the position of the third propodal article, therefore rendering segmental homologies equivocal. The basal article's apparent absence in most Peracarida may be regarded as i) multiple loss events, ii) a derivation of the Isopoda earlier than most other peracarid groups, or iii) insufficient data as seen in Cumacea and Amphipoda. A rudimentary antennal basal article is also present in some hypsimetopine phreatoicideans (research in progress). Because the basal antennal article is found in at least four major isopod taxa as well as some mysids, it appears to be a plesiomorphic feature within the isopods, and possibly in other peracarids. Other key taxa, such as the Mictacea and the Spelaeogriphacea, have not been carefully studied for basal article remnants, so perhaps we do not have the full story.

The morphology of the seventh pereonite and the male penes (Fig.3A,B) could be an apomorphy shared with the Asellota. Just & Poore (1992) show that the asellotan penes are derived from a coxal position: species of the genus *Vermectias* has a thin sclerite that connects the coxa with the penes. In *Tainisopus*, however, the coxal connection to the penes is broad and triangular, such that much of the ventral surface of the seventh pereonite appears to be composed of the coxa of

pereopod VII. Many higher isopods have ventral surfaces of coxal origin (Brusca & Wilson, 1991), and the expanded articulations of the coxae seen in *Tainisopus* may be a step in this direction. The penial morphology of *Tainisopus* may be intermediate between i) the primitive condition where the penes are on the coxae, ii) the asellotan condition where the penes are 'pinched off' still fully functional coxae, and iii) a more derived isopod condition where the coxae expand to cover the ventral surface, thereby carrying the genital pores medially and rendering the coxa-body articulation inflexible.

The broad coxa of pereopod V of the female also bears the oopore (Fig.3E), although it also has a fully developed oostegite, unlike the Phreatoicidea. A recent review of isopod female genitalia (Wilson, 1991) has suggested that the position of the isopod oopore on the ventral surface might have developed in a variety of ways, either as part of the lateral movement of the ventral coxal plate, or as a preliminary disassociation from the coxa and then a later penetration of the ventral coxal plate as it migrates medially over the ventral surface. In the Asellota, the oopore has become disassociated from the still movably articulated coxa. *Tainisopus* clearly has retained the primitive condition, found also in *Bathynomus* (unpublished observations), where the oostegite is still intimately associated with the coxa. The fifth pereonite coxa of the female, like the other pereonite's coxae, has become more intimately associated to the ventral surface and is not completely mobile. The coxae of *Bathynomus* seems to be much more mobile and freely articulated.

In conclusion, the above features militate against *Tainisopus* being members of the phreatoicidean clade. The diagnosis of the Phreatoicidea, currently a compact group, would have to be considerably diluted to include *Tainisopus*. The synapomorphies of the Phreatoicidea that are not shared with *Tainisopus* are as follows: pleotelson vaulted with uropods rotated ventromedially; pleotelson strongly flexed ventrally with a dorsally recurved tip (secondarily uncurved in ground water taxa); proximal and distal segments of pleopodal exopods, when separate, with narrow articulation; mandibular spine row on distinct medially projecting lobe; antenna with basal article of the protopod reduced or absent; antennula lacking rudiment of a second flagellum. Moreover, *Tainisopus* is also clearly not an asellotan. It lacks the specialised copulatory structures, such as the female spermathecal duct (cuticular organ), and modified pleotelson that defines the Asellota (Wilson, 1991; Brusca & Wilson, 1991). No asellotan can swim with its pleopods, while *Tainisopus* is a good swimmer. In many respects, the Asellota are highly derived compared to other isopods, and *Tainisopus* shares none of their specialisations. The features that *Tainisopus* shares with the asellotans (as discussed above) are probably plesiomorphies.

Therefore, we conclude that *Tainisopus* can be neither a phreatoicidean nor an asellotan. Unfortunately, the best classification is not immediately obvious because *Tainisopus* lacks specific synapomorphies of other isopod suborders. The generalised mouthparts are unlike the derived features seen in any of the higher isopod suborders ('Flabelliferan' families, Anthuridea, Epicaridea, Gnathiidea, Oniscidea + Calabozoidea, Valvifera), except for perhaps the Sphaeromatidae or some Oniscidea (disregarding the lack of a mandibular palp in the latter). We suspect that *Tainisopus* may have evolved prior to the evolutionary divergence of these suborders. The similarity of all body segments suggests a fair amount of generality, and therefore *Tainisopus* seems to retain presumed ancestral forms for any higher isopod.

Furthermore, the possession in *Tainisopus* of derived features common to all higher isopods is suggestive of an early derivation with the higher isopods. Such synapomorphies include the presence of true coxal plates and a pereopodal tagmosis (3-4, not 4-3: see Brusca & Wilson, 1991) similar to that seen in the Cirolanidae or other derived isopods. *Tainisopus* also has five pereopodal oostegites, while Phreatoicidea and Asellota never have more than four. Most higher isopods, from Cirolanidae to Epicaridea, have five pereopodal oostegites (a sixth may appear on the maxilliped), with some taxa having more; these (e.g., Cymothoidae) can be considered special apomorphies. Broad, strongly natatory pleopods are shared between *Tainisopus* and the higher isopods, while the phreatoicideans and asellotes are either poor swimmers, do not swim at all, or do so secondarily using their pereopods. A homology study of these and other characters in all isopods (research in progress) will recommend the most probable classification for *Tainisopus*.

Population biology. On a comparative basis, the body length measurements of the relatively undamaged specimens reveal the approximate size structure of *T. fontinalis* (Fig.13). The mancas present in the sample were of the latest stage (instar 3, showing a rudimentary pereopod VII), indicating that the young are released from the brood pouch at a size just below 2 mm. Sexual differentiation is apparently present by the fourth instar, and sexual maturity in both sexes is reached at a length of approximately 5.5 to 6 mm. There appears to be at least two different sizes of fully preparatory females (5.5-6.5 mm and 7.5-8.4 mm), with a distinct gap of brooding females in between (6.5-7.0 mm). Therefore, this species is iteroparous, with alternating preparatory and brooding instars in the females. The fully copulatory males cover a large size range, indicating that they continue to moult after reaching maturity, and also may breed several times. The presence of most life stages in this one sample suggests that breeding occurs almost continuously at this time of the year (June), despite the sample occurring at the beginning of the dry season. Continuous breeding, however, is common in subterranean animals, and the population at station

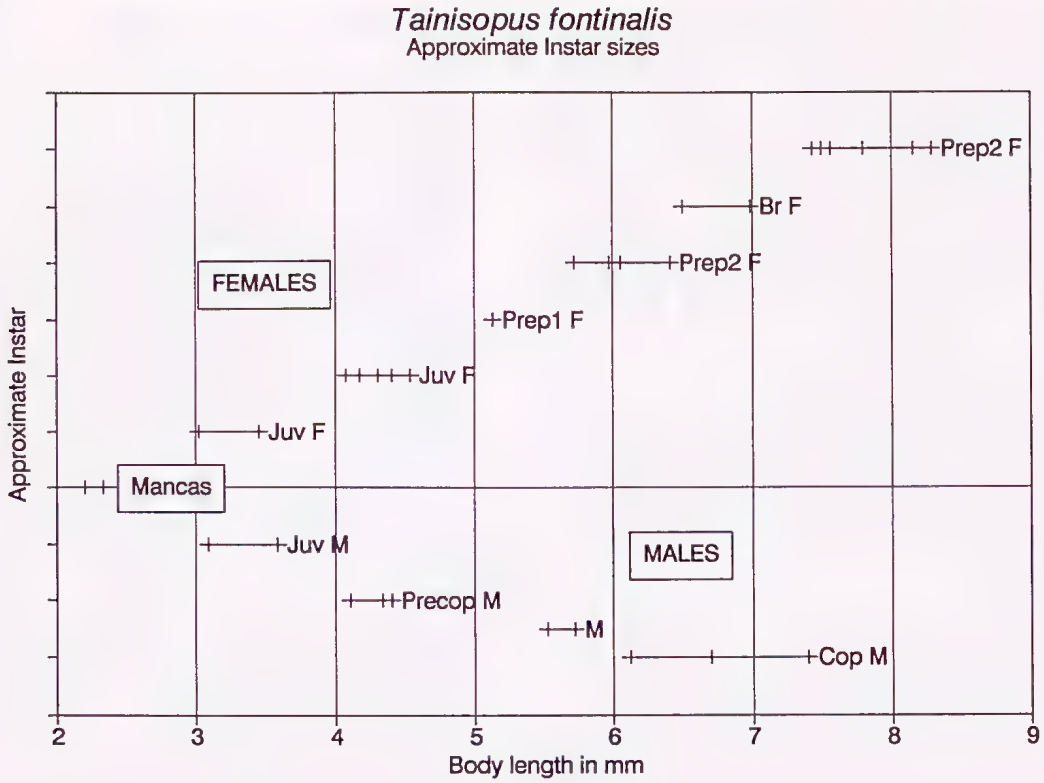

Fig.13. Approximate population size structure from sample K1 of *Tainisopus fontinalis* n.gen., n.sp. Horizontal bars mark the size ranges within approximate instars, and vertical tics mark individual size measurements. Abbreviations used in figure: Br - brooding; Cop - copulatory; F - female; Juv - juvenile; M - male; Precop - precopulatory; Prep1 - early preparatory; Prep2 - fully preparatory or copulatory.

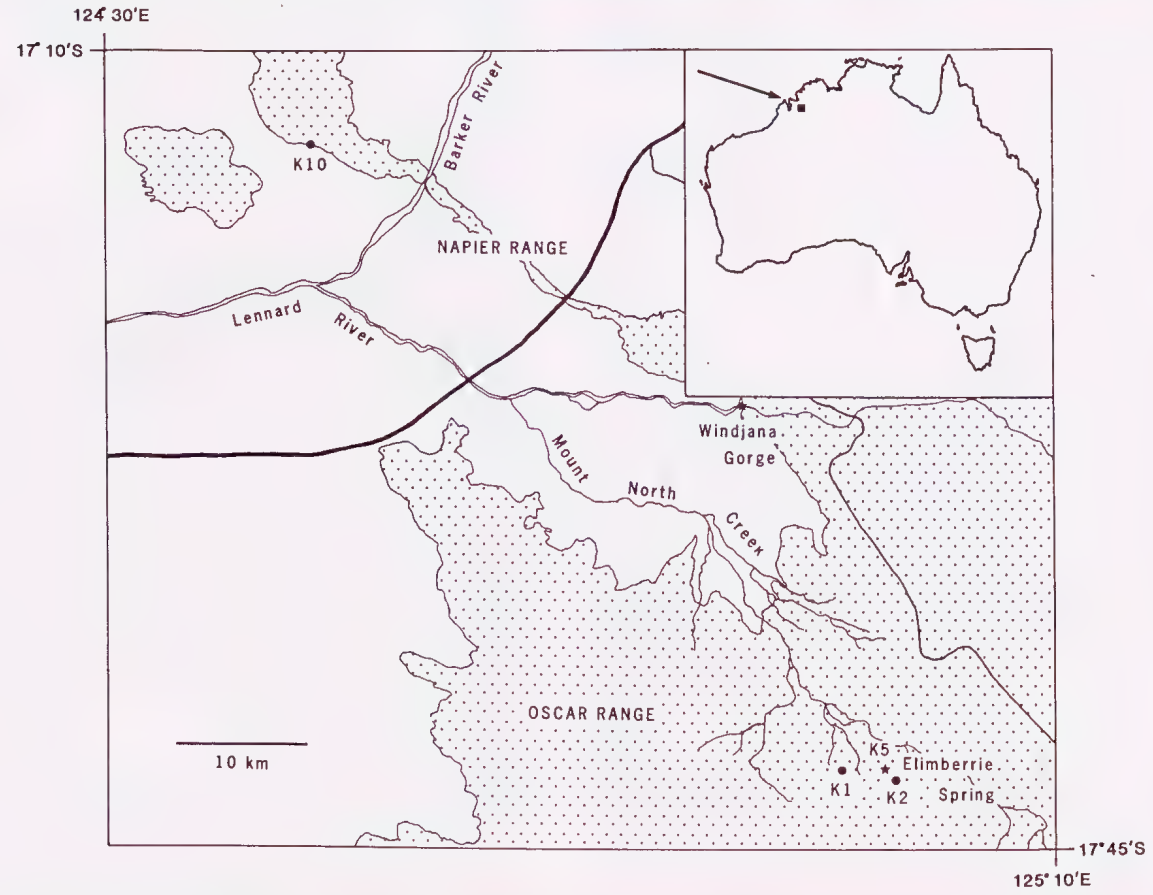

Fig.14. Map of *Tainisopus* localities in the Oscar and Napier Ranges, Kimberley Region, West Australia. In upper right inset, the arrow and small filled square indicates the Australian location of the map.

K1 is evidently largely subterranean.

Biogeography. The Kimberley Region has a tropical savanna climate with about 380 mm of rainfall in the southern part to about 890 mm in the northern part. Most of the rain falls between December and March, the region being arid with high evaporation for the remainder of the year. Ellaway *et al.* (1990) state that of the 650 mm annual rainfall in the region in which our material was obtained, 85% falls in the December-March period. Consequently all rivers except the lower reaches of the Ord River and spring fed streams in the Kimberley Plateau stop flowing in the winter months and even large water holes and most springs are only semipermanent (Dow & Gemuts, 1969). Water flow was presumably even more reduced during the arid Pleistocene glacials (e.g., DeDeckker, 1986). Under conditions of extreme aridity, aquatic invertebrates with poor dispersal powers probably only survived in subterranean water or springs fed from significant subterranean sources. With this in mind a survey of springs of parts of the Kimberley was carried out, primarily to collect molluscs and crustaceans. Of the numerous habitats collected, the four from which material is recorded in this paper (Fig.14) were the only ones to reveal unusual 'locally endemic' macrocrustaceans.

Tainisopus species are blind and may breed continuously, so this genus is clearly part of the Kimberley subterranean fauna. The limestone hills in which the springs and cave containing the isopods are found (see Fig.14) are Devonian coral reefs formed in a small embayment occupying the western edge of the Kimberley. No marine transgressions in this area have occurred since the Devonian (Veevers, 1984). Thus *Tainisopus* is not derived from a immediate marine ancestor, but is most likely of ancient freshwater stock. The only other relictual freshwater isopods known from Australia are mostly found in the south western and south eastern areas. The exceptions, however, are interesting. *Phreatomerus latipes* (Chilton, 1922) is an unusual relict phreatoicidean restricted to one group of artesian springs in northern South Australia (Ponder, 1986). *Eophreatoicus kershawi* Nicholls, 1926 has been found in a small pool at Sandstone Bluff (about 12°S 133°30'E), in Arnhem Land, NT (Nicholls, 1926, 1943). These species may be remnants of a period when Australia was more extensively covered with temperate rain forest and freshwater habitats were more prevalent. Owing to their highly restricted and patchy distribution, these isopods are among the Australian fauna's most potentially endangered invertebrate species (cf. Ponder, 1986). The difficulty of sampling in the Kimberley and in Arnhem Land of the Northern Territory, however, suggests that more collecting in these areas may uncover new species of these interesting relicts. The karst ground water system of the Oscar and Napier Ranges (Ellaway *et al.*, 1990) may also provide additional undiscovered habitats for *Tainisopus*.

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Cranial Anatomy of Two New Late Devonian Lungfishes (Pisces: Dipnoi) from Mount Howitt, Victoria

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ABSTRACT. Two new lungfishes are described from the Frasnian lacustrine sediments near Mount Howitt, eastern Victoria. *Howidipterus donnae* n.gen., n.sp. has toothplates with well-developed marginal teeth, and has a skull roof pattern similar to *Scaumenacia* but with a D bone present and large paired rostral bones anterior to the E bones. The cheek has moderately deep infraorbitals. The scales have a coarse ornament with widely spaced ridges. *Barwickia downunda* n.gen., n.sp. has a skull roof pattern characterised by a narrow, small D bone, narrow E bones as long as the C bones, and I bones which are indented well into the rear of the B bone and on occasion may contact each other. The dentition is denticulate as in *Fleurantia*. The cheek has a narrow, bar-like bone 6 + 7. The scales of *Barwickia* are finely ornamented.

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Lungfishes are one of the last groups of fishes to be studied from the diverse Mount Howitt fossil fish fauna which contains the following taxa: the placoderms *Bothriolepis gippslandiensis*, *B. cullodenensis* and *B. fergusoni* (Long, 1983a; Long & Werdelin, 1986), *Austrophyllolepis ritchiei*, *A. youngi* (Long, 1984) and *Groenlandaspis* sp. (Long, 1982); the acanthodians *Culmacanthus stewarti* (Long, 1983b) and *Howittacanthus kentoni* (Long 1986); the actinopterygian *Howqualepis rostridens* (Long, 1988a); the crossopterygians *Marsdenichthys longioccipitus* (Long, 1985) and *Beelarongia patrichae* (Long, 1987a), and the two new dipnoans described in this paper. In addition there are partial bodies of porolepiforms with *Glyptolepis*-type scales and a possible actinistian. The fauna represents one of the best preserved and diverse Late Devonian freshwater fish assemblages from a single site in the Southern Hemisphere, and is also significant in being the keystone for biostratigraphic correlations throughout eastern Victoria (Long, 1983a; Long & Werdelin, 1986).

This paper briefly describes the cranial anatomy of two new genera, based on examination of approximately 80 of the best preserved heads. The scales are described, as these are an important feature for distinguishing the two genera when the skulls are poorly preserved. Many additional specimens, now registered in the Museum of Victoria, would require further

preparation before detailed measurement of the postcranial skeleton could be made. Discussion of the phylogenetic relationships of the two new forms has been deferred until the complete anatomy of the fishes has been described.

Material and Methods

The Mount Howitt lungfishes are studied from latex casts of the natural moulds in black shale, so there are no details of toothplate histology available. The specimens are generally preserved as flattened, slightly disrupted carcasses, but often fine preservation of cartilage bones, such as elements of the visceral skeleton, are seen from latex peels. Photographs are of latex casts dusted with ammonium chloride. The description of the material follows terminology used by Miles (1977). Classification follows the new scheme of Campbell & Barwick (1990). Comparative material examined includes 3-dimensional lungfish skulls from the Gogo Formation of Western Australia held in the WA Museum and in the Geology Department, The Australian National University, Canberra.

Specimens are housed in the palaeontological collections of the Museum of Victoria, Melbourne (NMV), and the Western Australian Museum (WAM).

Abbreviations used in the figures are listed in the Appendix.

Systematic Palaeontology

Subclass **OSTEICHTHYES**

Infraclass **DIPNOI**

Suborder **Speonesydrionina**

Dipteridae Owen 1846

Remarks. Although the postcranial skeleton is to be described in a future work, it is suffice to say here that the new genus is placed in this family because of the presence of two dorsal fins, the anterior dorsal fin not being reduced as in *Scaumenacia* and *Phaneropleuron* (Phaneropleuridae). However, the modification of the second dorsal fin (in being larger than the first dorsal fin), and the loss of cosmine, indicates that this new form is more derived than *Dipterus*.

Howidipterus n.gen.

Type species. *Howidipterus donnae* n.sp.

Etymology. After Mount Howitt and the well-known genus *Dipterus*.

Diagnosis. A lungfish having a maximum body length up to 0.5 m. Skull roof approximately 82% as broad as long, and dermal bone pattern highly variable; general configuration with B bone one third as long as skull; C bones equidimensional with E bones; (both E and C being as long as B). D small, being about half the length of the C bones, and about two thirds as broad as long. Paired rostral ossifications anterior to E bone, rest of snout unossified. Occipital commissure passes through A bone. Cheek with deep 1A+B bone, separate small 1C bone. Pterygoid toothplates elongated, subtriangular in form with up to 17 toothridges. Toothridges terminate in the mesial half of each toothplate which has a concave surface, but isolated cusps may be present in this region. Small, narrow anterior median toothed bone present anterior to upper jaw toothplates. Parasphenoid with a diamond-shaped corpus half total length of bone and lacking a buccohypophysial foramen. Externally exposed regions of scales bearing widely-spaced thin bony ridges.

Remarks. The above diagnosis separates *Howidipterus* from the few other known Devonian dipnoans possessing toothplates and a D bone (e.g., *Dipterus*, *Chirodipterus*, *Scaumenacia*, some specimens of *Rhinodipterus secans*) by the unusual morphology of the toothplates, absence of cosmine, general proportions of the skull roof and, where known, the body and fin shape. Most post-Devonian forms which retain a D bone (e.g., *Scaumenacia*, *Ctenodus*, *Tranodis*, *Conchopoma*) are distinguished from *Howidipterus* by having a shorter broader skull roof, the occipital commissure passing through the much enlarged B bone, and the coalescence of the two dorsal fins and anal fin into a diphycercal caudal fin. *Delatitia*, which also retains bone D, does not have the commissure in B and is distinguished by skull roof proportions.

Howidipterus donnae n.sp.

Figs 1-11, 20A

Etymology. For Donna Long, who diligently assisted in field work at Mount Howitt.

Material. HOLOTYPE, NMV P181884, a cranium showing little abnormal fusion or space capture between skull roof elements (Fig.1A). PARATYPES, NMV P181877 (showing tooth plates, Fig.1B), and NMV P181806 (showing ventral skull bones and lower jaw, Fig.3D). Other material (all NMV specimens): P172632, P181788-P181810, P181860-P181867, P181869-P181873, P181875, P181878-P181883, P181886-P181889, P186574, P186568, P186570. Many other specimens which have not yet been registered are in the Zoology Department, Monash University.

Locality and age. Mount Howitt spur quarry, lower

mudstone, Avon River Group (Long, 1983a, fig.1). Late Devonian (Frasnian), lacustrine facies.

Diagnosis. As for genus, only species.

Description. *Skull roof.* The skull roof bones of *Howidipterus* show considerable variation (Figs 1-5), resulting from fusion and/or space capture, as in most dipnoans. Because of this the description will be based largely on specimens showing the unfused pattern of skull roof elements (e.g., seen in the holotype Fig.1A). A restoration of the head, based on the best specimens, is shown in Figure 6. Cosmine is not present on the skull roof or any other dermal bone, as seen in specimens with some surficial bone preserved. The posterior skull bones are thicker than the anterior and lateral elements. Surface ornamentation consists of low radiating ridges and isolated small tubercles on skull roof bones, with extensive pitting on some of the circumorbital series carrying the infraorbital sensory line. On average the breadth of the flattened skull roof is about 82% of its length.

Bone A is short, occupying 8% of the skull roof length. Its width is twice its length (Fig.1A,D). Bone B occupies about 25% of the skull length, is raised in its centre and lacks a median thickening on the visceral surface (Fig.1C). The middle and posterior pit-line grooves may both converge towards the centre of B. The occipital sensory-line canal passes from I through to A as in most other Devonian dipnoans. The length of each C bone is more than

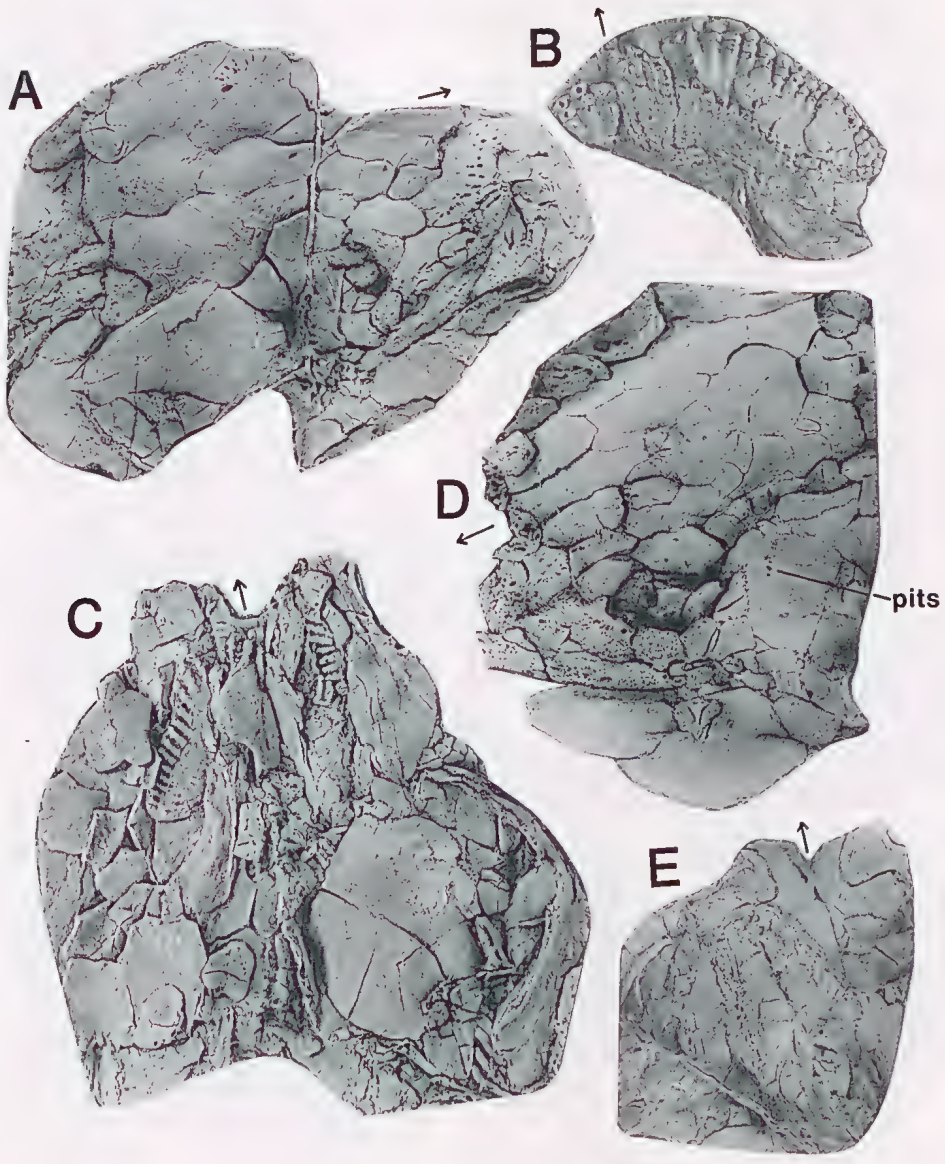

Fig.1. *Howidipterus donnae* n.gen., n.sp. arrow indicates median line and anterior direction. A, holotype NMV P181884, skull and cheek, X1. B, paratype NMV P181877, showing pterygoid toothplates, X1.5. C, NMV P 181799, showing skull roof in visceral view and pterygoid tooth plates, X 1.5. D, NMV P 181886, showing skull roof and cheek, X1.5. E, anterior part of skull of NMV P181883 showing rostral bones, X2.

twice their breadth and slightly longer than B, occupying 30% of the skull roof length. C bones laterally contact J, K, L and some contact M bones, and anteriorly contact the D and E bones. The E bones are narrower and shorter than C bones, and occasionally are divided into anterior and posterior

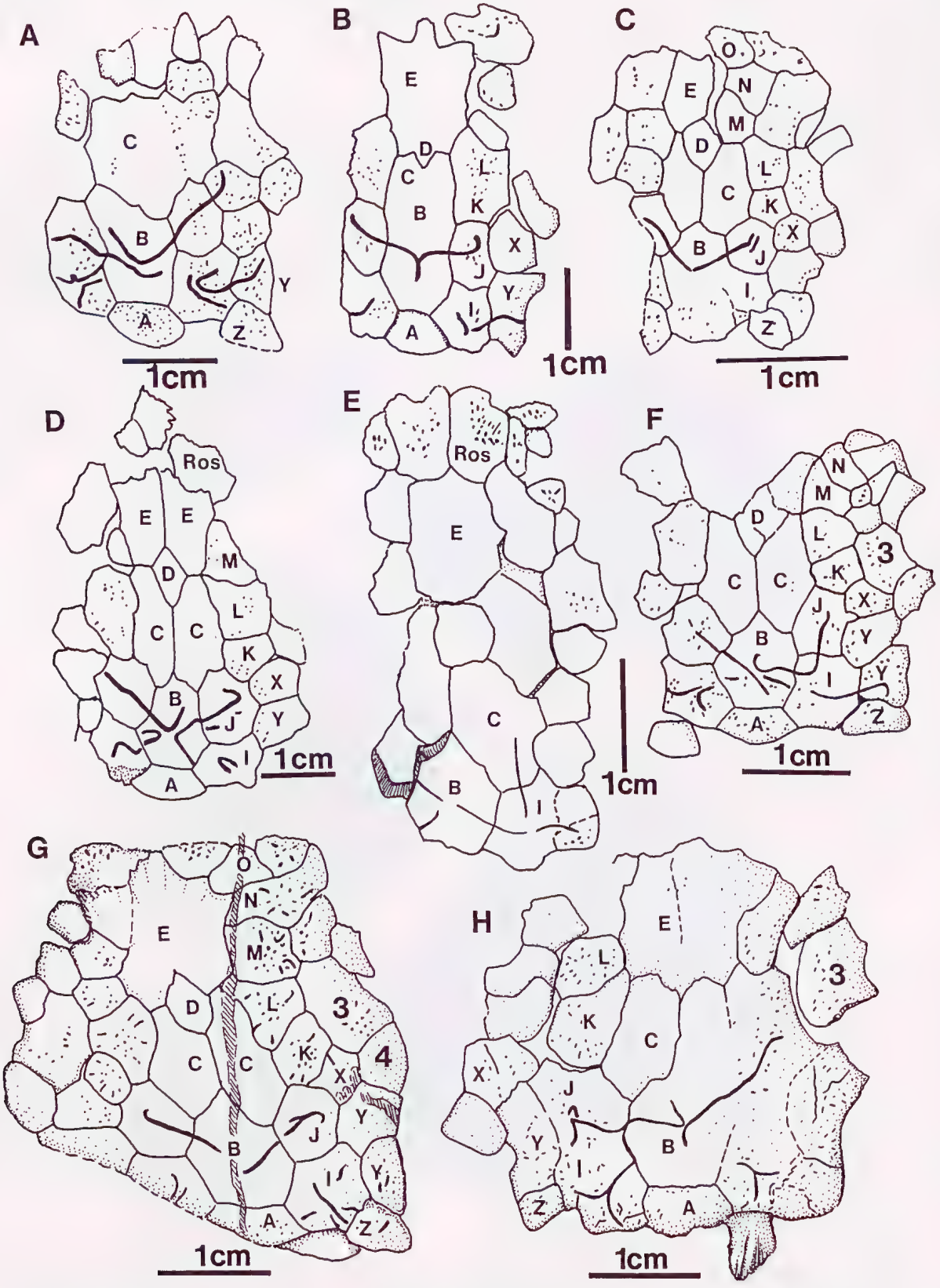

Fig.2. Unusual variations in the skull roof patterns, in dorsal view, of *Howidipterus donnae* n.gen., n.sp. A, NMV P181804. B, NMV P181790. C, NMV P181791. D, NMV P181884. E, NMV P181796. F, NMV P181802. G, NMV P181803. H, NMV P181809.

elements, or fused together (Fig.2B,E) or fused with other lateral bones (Fig.2G,H). Bone D is stable, rarely being subdivided (e.g., P181790). It is quite small, and broad for its length relative to the other roof bones.

The supratemporal series (X, Y1, Y2) occupy about 40 to 45% of the skull roof length. Y2 generally has a strong posterolateral projection which flanks most of Z. There is often a deep notch between Y1 and Y2. Y1 bears a thickening on the visceral surface where it contacted the top of the lateral commissure as in *Chirodipterus*. Y1 has a weak depression in its posterior half so that the visceral thickening becomes prominent, presumably for contact with the dorsolateral cristae of the neurocranium as in *Chirodipterus* (Miles, 1977).

A maximum of seven elements has been recorded on the supraorbital lateral line canal (P181800) but commonly there are four or five: K, L, M and N, and subdivisions of these. In the extrascapular series there are three bones usually present: Z, A, Z. In some specimens there appears to be a small bone present behind A and Z, possibly the G bone. It is very thin compared to the other extrascapulars. Posterior to Z on some specimens there is an element carrying the lateral line canal which is here

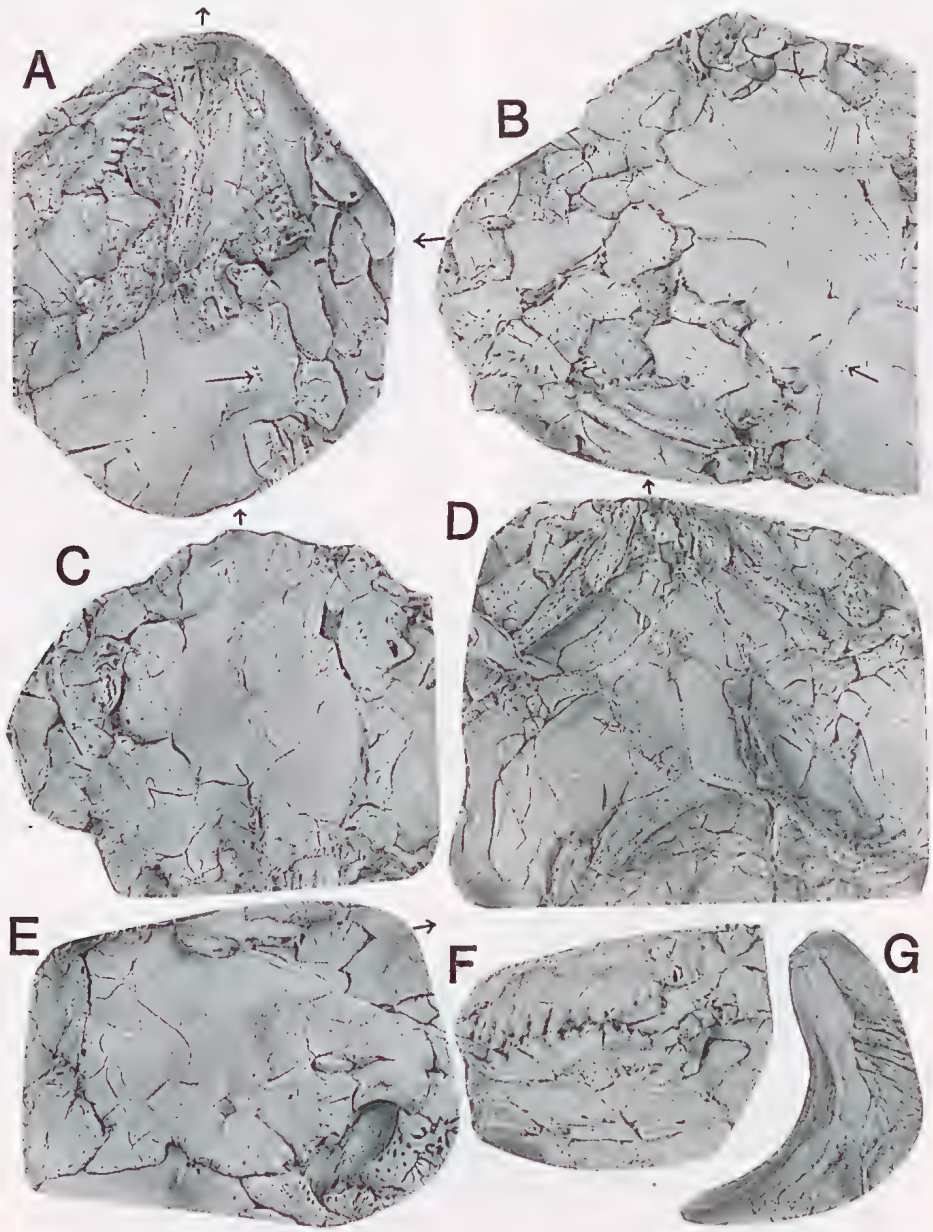

Fig.3. *Howidipterus donnae* n.gen., n.sp., arrow indicates median line and anterior direction. A, NMV P181863, showing pterygoid toothplates and lower jaw, x2. B, NMV P181880, showing skull roof and cheek, x1.5. C, NMV P181809, showing skull roof and cheek, x1.5. D, paratype NMV P181806, showing skull bones in ventral aspect, including both lower jaw rami, x1.3 . E, NMV P181805, skull roof in dorsal view, x1.5. F, NMV P181888, showing upper and lower jaw dentition in occlusion, visceral aspect, x2. G, cleithrum and clavicle of NMV P181883, x2.

interpreted as a post-temporal. It is an external bone and lacks forward processes, thus distinguishing it from the subdermal anocleithrum of other Dipnoi (e.g., *Scaumenacia* Jarvik, 1980; *Eoctenodus* Long, 1987b). An anocleithrum has not yet been seen in the material of *Howidipterus*.

Cheek. The circumorbital series normally comprises bones 1 to 7, and these are relatively high as in *Dipterus* or *Scaumenacia*. In some cases bone 7 may be absent as an independent element and bone 4 may be excluded from the orbital margin. Posterior to bone 5, bones 8 and 9 are constantly present and partially overlie the operculum. The region ventral to bone 9 is rarely well preserved but it appears that there are normally 3 to 7 elements of approximately the same size (Figs 10, 9b-9g), these being just a little smaller than bone 9a. Bone 1a+b is rather deep anteriorly and can be readily used to distinguish *Howidipterus* from *Barwickia*, in which this element is very narrow. A small bone 1c is present as in *Chirodipterus* (Miles, 1977; Campbell & Barwick, 1982). Dorsal to bone 2 bone 0 is usually present. The space normally occupied by these elements may, however, be occupied by a single bone (e.g., P1818000) or the 0 space may be captured by supraorbital lateral line elements (e.g., P181794, P181795).

Snout. The tip of the snout and its ventral surface with narial grooves is not seen in any specimen and was probably unossified. There are two separate rostral elements (Ros) that meet in the midline on the dorsal surface of the nasal capsule; these elements carry a loop of the supraorbital sensory line.

Sensory line system. The lateral line system of the skull roof of *Howidipterus* is developed as normal for other Middle and Late Devonian dipnoans (e.g., *Scaumenacia, Dipterus, Rhinodipterus*; Lehman, 1966; Stensiö, 1947; White, 1965). Bone 3 carries a short anterior extension of sensory line canal from bone 4. Pit lines are well developed on the skull roof, cheek and gulars. They are deeply incised into the dermal bones, and often show irregularities in their course.

Palate. The palate is not completely preserved on any one specimen, but it can be reconstructed using a number of specimens (Figs 1C,3A). Most specimens show just the pterygoids and upper toothplates. Where the parasphenoid is preserved it is composed of very thin, cancellous bone. It is of normal shape for a Late Devonian dipnoan having a stalk and a rhombic corpus, the latter comprising about half the total parasphenoid length. The buccal surface of the corpus is smooth apart from a median thickening where the stalk meets the corpus, as in *Eoctenodus* (Long, 1987b). The region where the buccohypophysial foramen is expected to be found is not preserved on any specimen, and the anterior end of the corpus is here reconstructed from its adjacent contact with the pterygoids.

The posteromesial margins of the pterygoids are gently concave and the boundary with the parasphenoid well marked. There is a small anterior median bone (Campbell & Barwick, 1984; vomer, Miles, 1977) present in a few specimens (Fig.7), here labelled as the vomer. It is a very narrow, curved element which bears rounded tubercles. It does not appear to be paired, so it is assumed to be a median bone and reconstructed in this position (Fig.8).

Lower jaw. Although the lower jaw is present in many specimens the symphysial region is usually poorly preserved and the glenoid fossa has not been observed (Fig.9). Specimen P181880 indicates that lower jaw was probably close to 65% of the skull length. The angular is the largest element in the lower jaw, occupying about half its length. It has two distinct regions: a thick section forming most of the ventral and some of the lateral face of the lower jaw, and a thin ascending lamina which occupies most of the lateral and some of the ventral face posteriorly. The surface of the former is pitted and meets the post-splenial at a V-shaped suture. The course of the oral and mandibular sensory-line canals

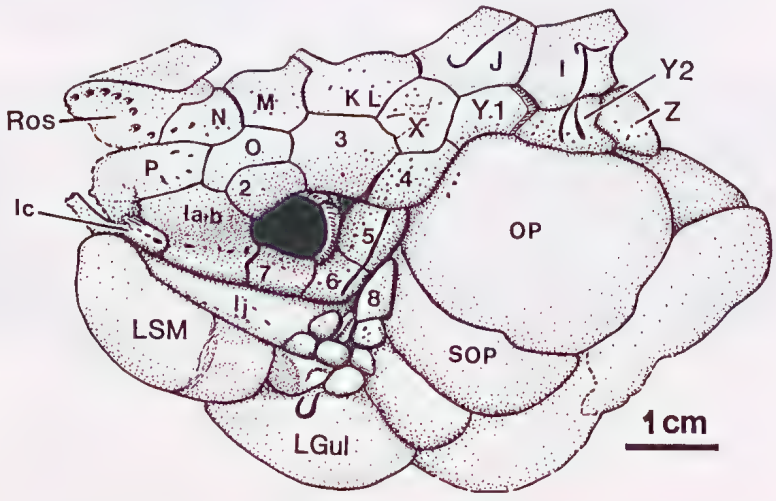

Fig.4. *Howidipterus donnae* n.gen, n.sp. Head of NMV P181799 showing well-preserved cheek bone pattern, lower jaw and ventral bones of the head.

is marked by very large, irregularly-shaped pores. The postsplenial is much shorter than the angular, and has a similar external appearance. An elongate depression on the lateral face indicates a labial pit extended back onto the postsplenial. The postsplenial is gently concave where it joins anteromesially with the splenial. The anastomosis between the mandibular and oral sensory line canals is visible on P181806, represented by two large, elongated pores. The internal face of the postsplenial is hollowed out along its entire length for the Meckelian cartilage. In all specimens showing this there are two foramina with grooves running a short distance posteriorly. These correspond to those identified by Thomson & Campbell (1971) on *Dipnorhynchus* as for the first efferent branchial artery and the anterior ramus intermandibularis V, and the second foramen for the ramus mentalis internus VII and the ramus alveolus VII. In *Howidipterus* these foramina are of about equal size.

The splenial is a small, 5-sided element, the longest edge forming the mesial suture with its antimere. Only one example of the dentary is seen in the material (P181799). It is clearly a paired element, as in *Uronemus* and possibly *Conchopoma* (Watson & Gill, 1923). The surface of the dentary is quite smooth, like the ascending lamina of the angular.

The prearticular is divided into a thick section bearing the dentition and a thin descending lamina which forms most of the mesial face of the jaw. The descending lamina is smooth, and bears four large foramina and numerous smaller foramina just dorsal to

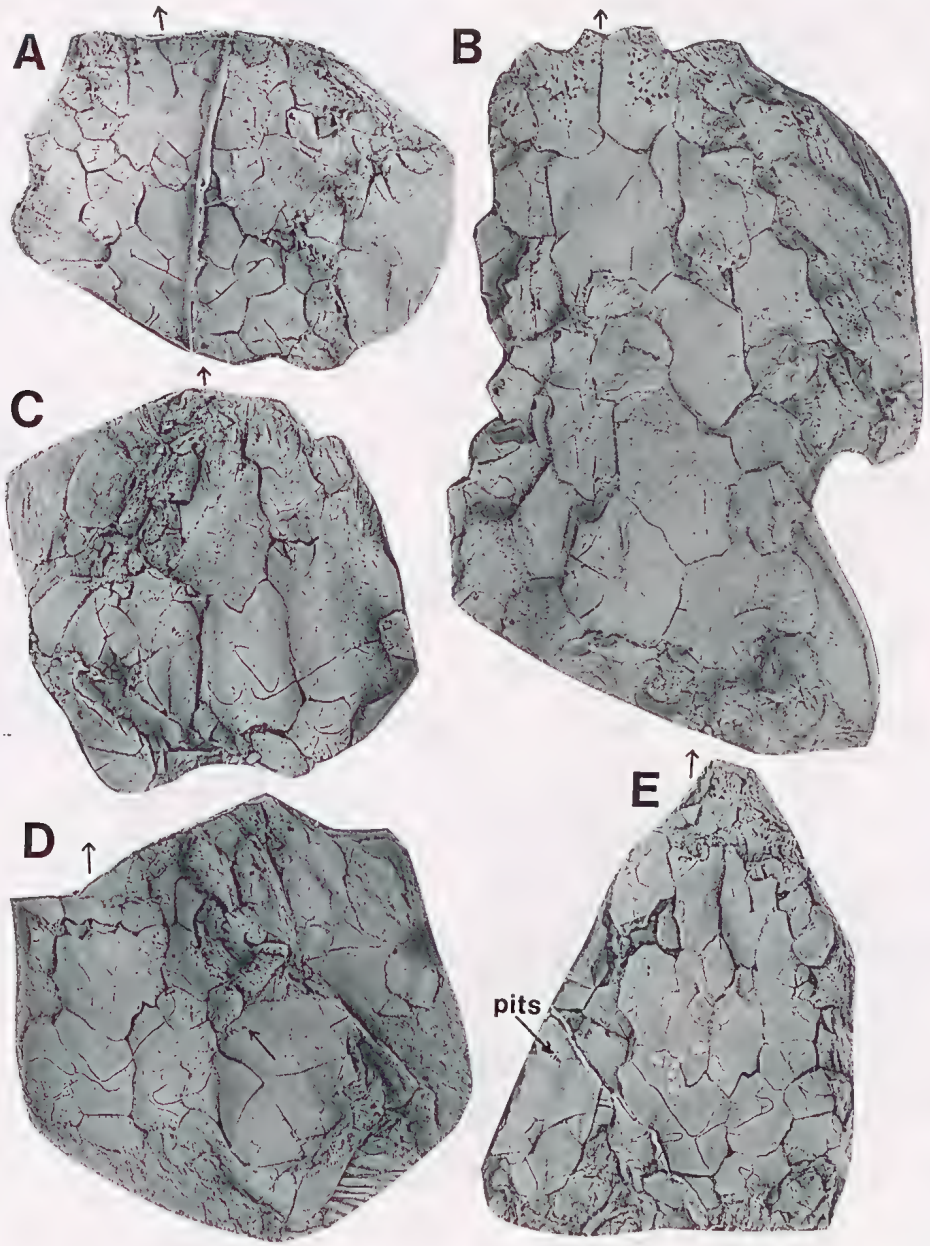

Fig.5. *Howidipterus donnae* n.gen., n.sp., arrow indicates median line and anterior direction. All are skull roofs in dorsal view, some also showing cheek bones. A, NMV P181803, x1.5. B, NMV P181796, x1.5. C, NMV P181882, x1.5. D, NMV P181804, x1.5. E, NMV P181884, x1.5.

the exposed area of the Meckelian cartilage. The extent of the Meckelian vacuity into which the adductor mandibulae muscles inserted cannot be precisely determined as it has been crushed posteriorly by bone 6 on the best specimen (P181799). It appears to have been rather small, and a moderate-sized preglenoid process was present for additional muscle attachment (Fig.9B,C).

Dentition. The dentition of *Howidipterus* is unusual for dipnoans. The upper toothplates show radiating rows of tooth ridges that vary in number from ten to 17 with growth. In some specimens the dentine has been worn away and the base of the cusps can be seen to be composed of bone, as in *Scaumenacia* (Denison, 1974). The functional part of the toothplate comprised three to five cusps only in each tooth row, and most

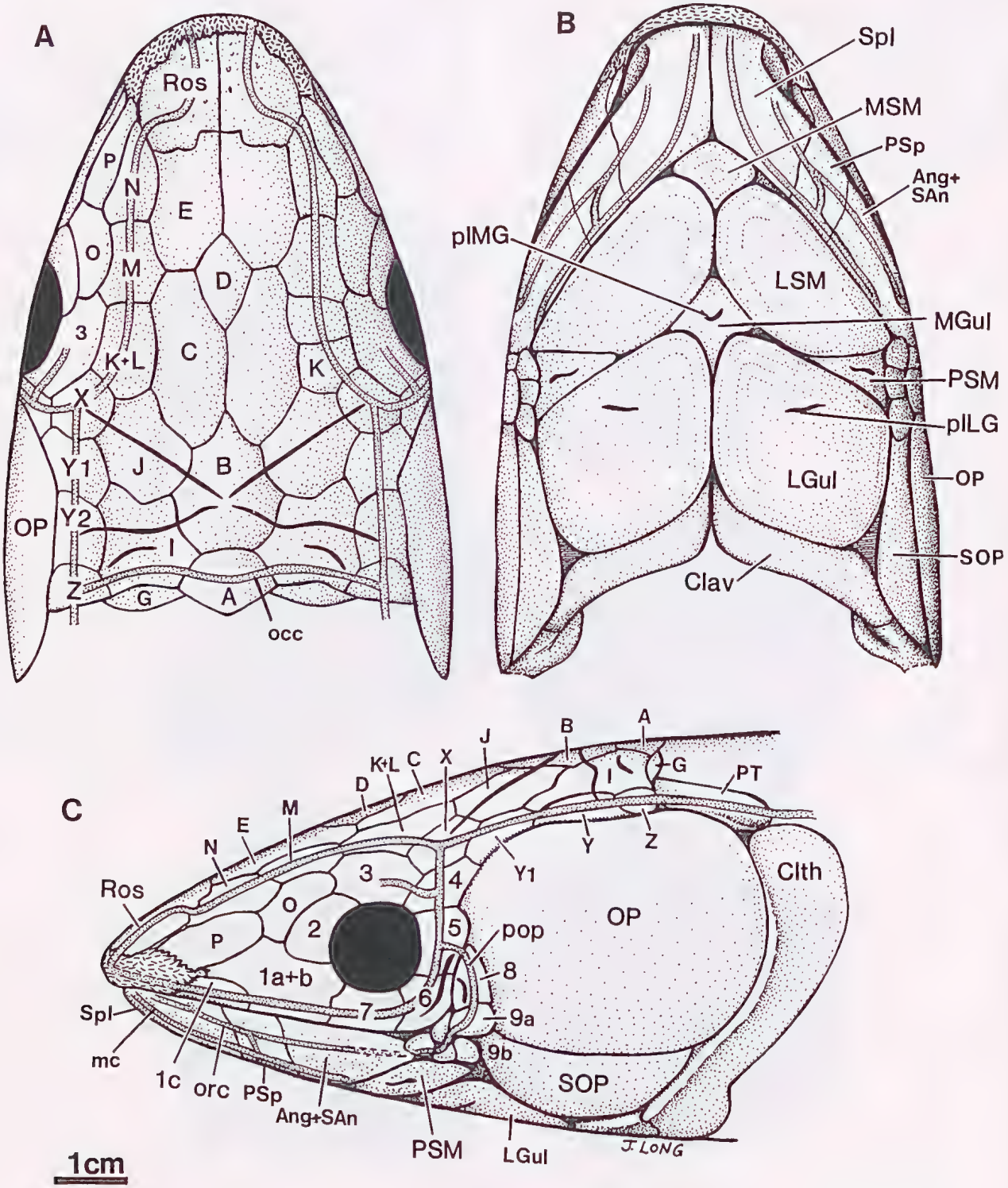

Fig.6. *Howidipterus donnae* n.gen., n.sp., reconstruction of the head in A, dorsal, B, ventral and C, lateral view.

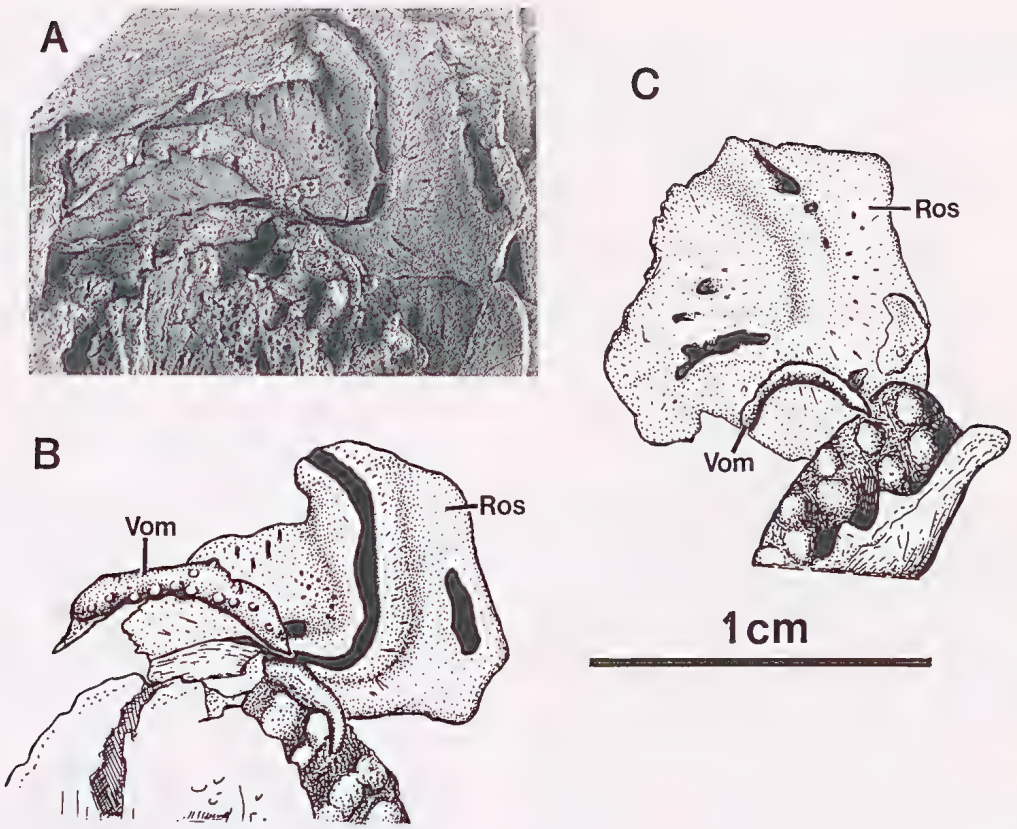

Fig.7. *Howidipterus donnae* n.gen., n.sp. A, B, NMV P181883 showing anterior toothed bone (vomer, Vom). C, NMV P181880, also showing vomer.

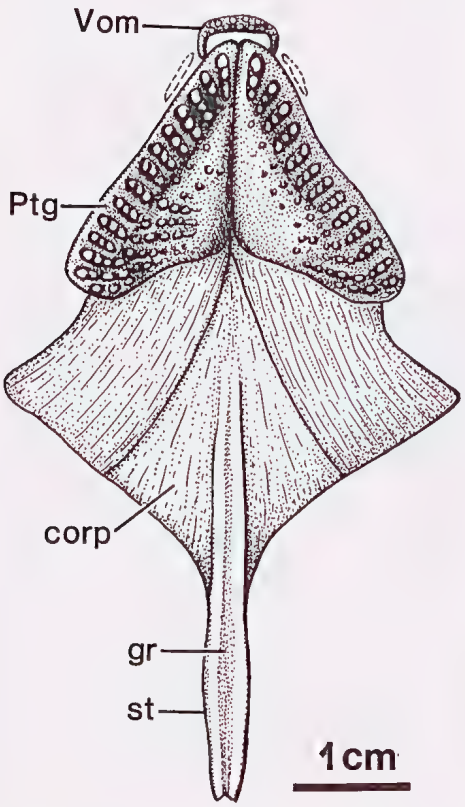

Fig.8. *Howidipterus donnae* n.gen., n.sp. reconstruction of palate showing pterygoid toothplates and parasphenoid.

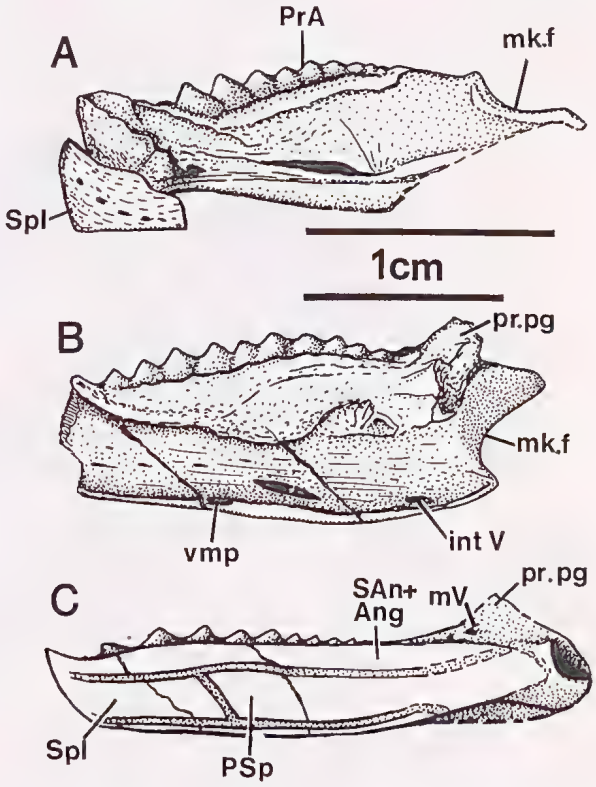

Fig.9. *Howidipterus donnae* n.gen., n.sp. Lower jaw bones. A, B, internal views. A, NMV P181792. B, NMV P181888. C, reconstruction of left ramus of lower jaw in lateral view.

of the area mesial to these functional cusps is worn down to a level much lower than the margins of the toothplate. Some secondary cusps may be present on this wear surface, which do not fit in with the radiating pattern of the cusp rows. The functional teeth are close together in each row. The teeth terminate mesially very abruptly, with worn teeth mesial to the functional teeth not usually preserved at all. Wear pits between teeth are generally not deep. The dentition of the anterior median bone, or vomer, comprises small peg-like teeth arranged in across the bone (Figs 6,7). The prearticular dentition is essentially the same as that of the pterygoids.

Operculogular bones. The operculogular series of *Howidipterus* is well represented. The operculum is a large, thick, more or less rounded bone, being clearly longer than high. There is a slight anterodorsal process which fits into a notch between the Y elements as in *Delatitia* (Long & Campbell, 1985). Some specimens show quite large foramina or surficial pits in the bone on the external surface of the operculum, numbering between 3 and 8 (Figs 1A,C,D; 3A,B; 5E). These can also be seen on the visceral surface, but their function is unknown. The subopercular 1 is shorter than the operculum, slightly thinner and about one third as high as that bone. About 40% of this bone was overlain by the operculum. There is a raised area with large pits on the visceral surface of P181806, possibly correlating with the "...distinct pit with roughened surface..." and the "...well defined knot of bone..." reported for *Griphognathus* and *Holodipterus* by Miles (1977: 253, 256). This feature is more posteriorly placed than in the two Gogo forms. Miles considered this area as possibly for attachment of the hyosuspensory eminence of the neurocranium. Subopercular 2 is poorly represented in the material, being mostly covered by the principal gular. It is somewhat triangular in form, not as long as subopercular 1 but with approximately similar exposed surface area (Fig.4).

The lateral gular is the second largest bone of the skull apart from the operculum. It is of trapezoidal shape with rounded corners, and there are overlap areas along the anterolateral edge for the two submandibulars. There is no evidence that the gulars overlapped each other very extensively, as in other dipnoans (*Speonesydrion, Dipterus, Scaumenacia*; Campbell & Barwick, 1984b; Westoll, 1949). The median gular is small, rounded anteriorly and drawn out posteriorly. When overlapped by the submandibulars and gulars only a small diamond-shaped area of the median gular is exposed. The lateral submandibular plate is suboval in shape, somewhere between the shapes of the bone in *Dipterus valenciennesi* and *Scaumenacia*. The posterolateral submandibular is triangular with rounded edges as in *Scaumenacia* and *Chirodipterus australis*. Anterolaterally it bears a large overlap area for the lateral submandibular plate. The median submandibular is a small diamond-shaped bone with two cuspate pitlines (Fig.10).

Scales and surface ornament of bones. The surface of the skull roof bones has a fine pustular ornament with radiating grooves present near bone margins (Fig.11). The scales have a surface ornamentation of

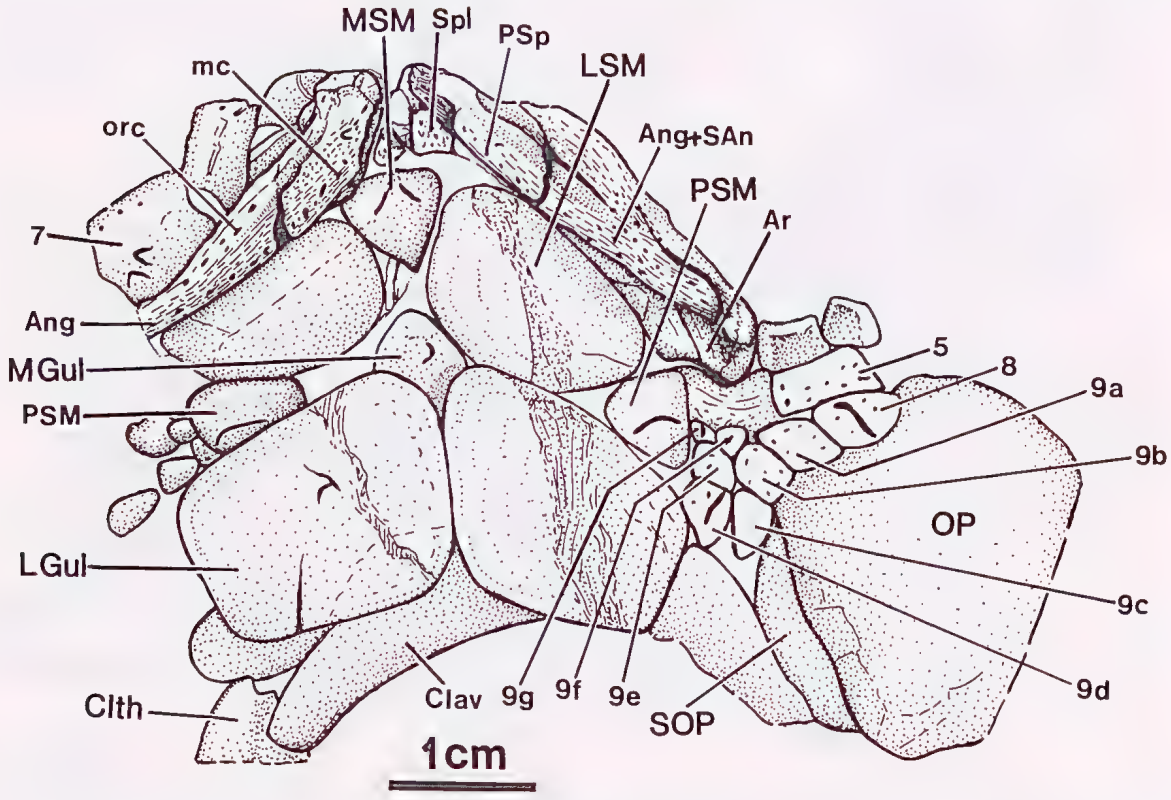

Fig.10. *Howidipterus donnae* n.gen., n.sp. NMV P181806, showing ventral bones of the head.

gently curved thin ridges of bone which are widely spaced, with smaller curved ridges occurring between them (Fig.20A). In this respect they are not 'packed' with radiating ridges as in *Scaumenacia* nor are they considered sparsely ornamented as described in *Eoctenodus* (Long, 1987b). In general the coarser ornamentation of the scales of *Howidipterus* make is easy to distinguish from the finer ornamentation of the scales on *Barwickia*.

Suborder **Uranolophina**

Fleurantiidae

Remarks. The family Fleurantiidae includes *Fleurantia* and *Jarvikia*, both of which share a skull with an elongate snout, a large single snout bone anterior to the C bones, and one large bone lateral to C incorporating K, L and M bones. The body is well known in *Fleurantia*, but not at all for *Jarvikia*. The new genus is provisionally assigned to this family because it shares a similar body plan to *Fleurantia* with one enlarged dorsal fin (the posterior one), and has a similar cheek bone pattern to *Fleurantia* with bone 10 lost from the cheek unit (unlike the rhynchodipterids *Griphognathus* and *Soederberghia*, Miles, 1977; Lehman, 1959).

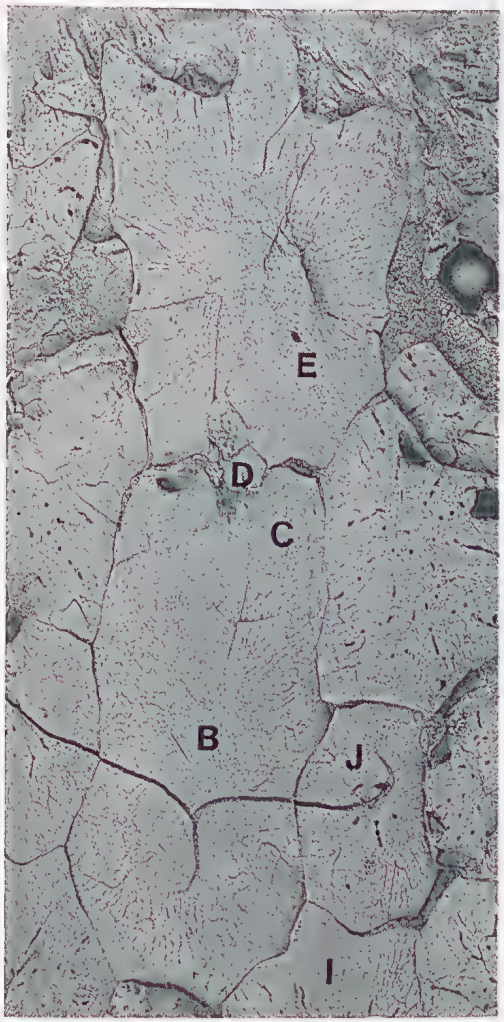

Fig.11. *Howidipterus donnae* n.gen., n.sp. Detail of surface bone ornamentation, NMV P1181790.

Barwickia n.gen.

Type species. *Barwickia downunda* n.sp.

Etymology. In honour of Dr Richard Barwick, Zoology Department, The Australian National University, for his contributions to the study of fossil lungfish.

Diagnosis. A dipnoan having a denticulate dentition and a skull roof which is about 60% as broad as long with a large B bone, indented posteriorly for the I bones: D small, sliver-like; C bones as long as B but considerably narrower; E bones elongated, often shorter and narrower than C bones. K absent. Infraorbital bone 6 very elongated, incorporating bone 7. Rostral bones anterior to E bones are absent. Body shape and fin disposition as for *Fleurantia*.

Remarks. *Barwickia* is readily distinguished from the only other Devonian dipnoans having a denticulate (i.e., denticle-shedding) dentition by its body shape, short snout and skull roof pattern. It differs from *Fleurantia* in the skull roof retaining a D-bone, by the shorter snout, and several details of the postcranial skeleton (not yet described, author's observation). It is readily distinguished from *Howidipterus*, not only by the presence of tooth-plates in the latter form, but also particularly by the skull roof having narrow E bones and lacking rostral ossification, by the very slender 6+7 bone below the orbit, and by having scales with finer ornamentation.

Barwickia downunda n.sp.

Figs 12-19, 20B

Etymology. A fortuitous collocation of letters.

Material. HOLOTYPE, NMV P181782, a good skull and cheek, with counterpart showing the palate and dentition (Fig.14). Other NMV specimens: P181780-P181787, P181868, P181874, P181876, P181885, P181890, P186566, P186567, P186573, P186575-77, P181579. WAM material: 90.7.1-90.7.7.

Locality and age. From Mount Howitt, in the lower mudstone, Avon River Group. This genus is more prevalent in the upper sections of the Mount Howitt fish beds exposure (snig track-"J" localities, about 50 m due east of main quarry, as marked in Long, 1983a, fig.1, "locality 8"). Upper Devonian (Frasnian).

Diagnosis. As for genus, only species.

Description. As in *Howidipterus* there is no evidence of cosmine in the dermal skeleton of *Barwickia*. The bones, particularly the anterior elements, are rather thinner than for the previous genus, and the ornamentation is much finer, consisting of pits and fine radial striae.

Skull roof. The skull of *Barwickia* is about 60% as broad as long (Fig.13), and the pattern of skull roof bones is notably less variable than for *Howidipterus*. In one example (WAM 90.7.7, Figs 12D, 13C) there is an unusual abnormality in which the I bones meet mesially behind the B bone, a condition otherwise seen only in primitive Early Devonian lungfishes (*Uranolophus, Dipnorhynchus* and *Speonesydrion*; Schultze & Campbell, 1987; Campbell & Barwick, 1987).

Bone B is about 30% of the skull roof length, and is indented posteriorly for the I bones. It bears a well-developed occipital flange, also found on the I bones, for overlap of the A bone, and anteriorly is a well-

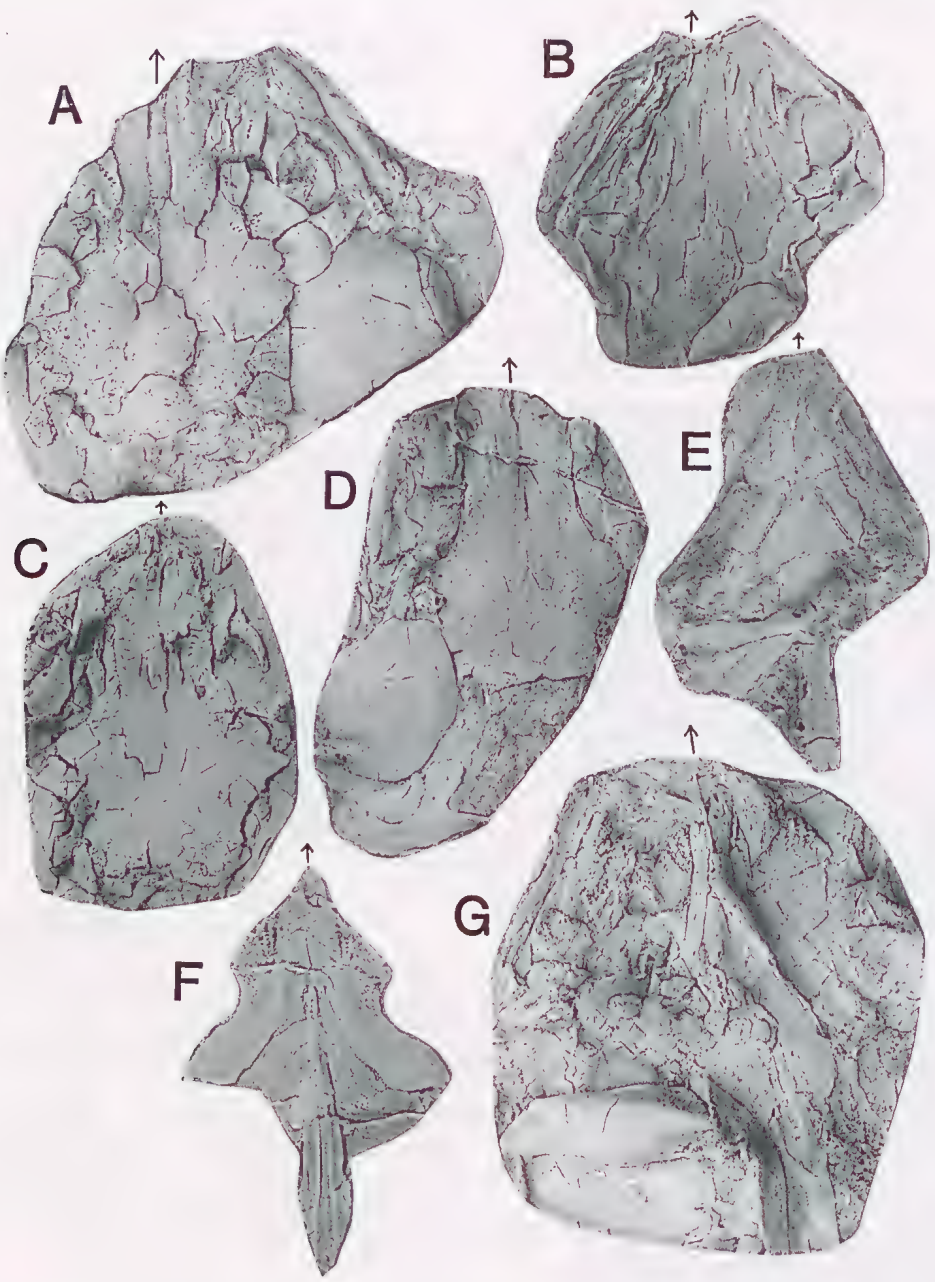

Fig.12. *Barwickia downunda* n.gen., n.sp., arrow indicates median line and anterior direction. A, G, WAM 90.7.1, showing (A) skull roof, cheek and lower jaw in external view, x1.5; and (G) aspects of the visceral skeleton and upper jaw dentition, x2. B, NMV P181780, showing skull roof and cheek in visceral view, x1. C, NMV P186566, showing skull roof, x1.3. D, WAM 90.7.1, showing abnormal skull roof pattern with I bones in mesial contact behind B bone, x1.5. E, NMV P181868, showing parasphenoid and pterygoids in ventral view, x1. F, NMV P181780 showing parasphenoid and ptergoids in dorsal view, x1.

developed point inserted between the C bones. Although B lacks a median thickening on the visceral surface, the Y1 and Y2 elements have thickenings for the quadrate and dorsolateral cristae of the braincase. The C bones are long but much narrower than the B bone. They are thin, as many specimens show postmortem cracking of these bones. Occasionally the C bones may be extended to occupy the E space (P181780, WAM 90.7.7, Fig.13C). The E bones are elongate and narrower than the C bones, and may terminate at an irregular anterior margin. In some cases, the C and E bones have fused (Fig.13B,C). There is no evidence of separate rostral bones anterior to E bones, nor any evidence that the snout was ossified. The D bone is very narrow, and is absent in one specimen (P181786). The supratemporal series is slightly longer than for *Howidipterus* due to longer Y bones. There is no notch between the Y bones, and the posterolateral projection of Y2 is weakly developed. The supraorbital lateral line series generally contains 3 or 4 bones: K, L, M, N or fused variants of these bones. M is particularly long and in some specimens fits into a V-shaped notch between L and C (Fig.13D). N is small and has an irregular

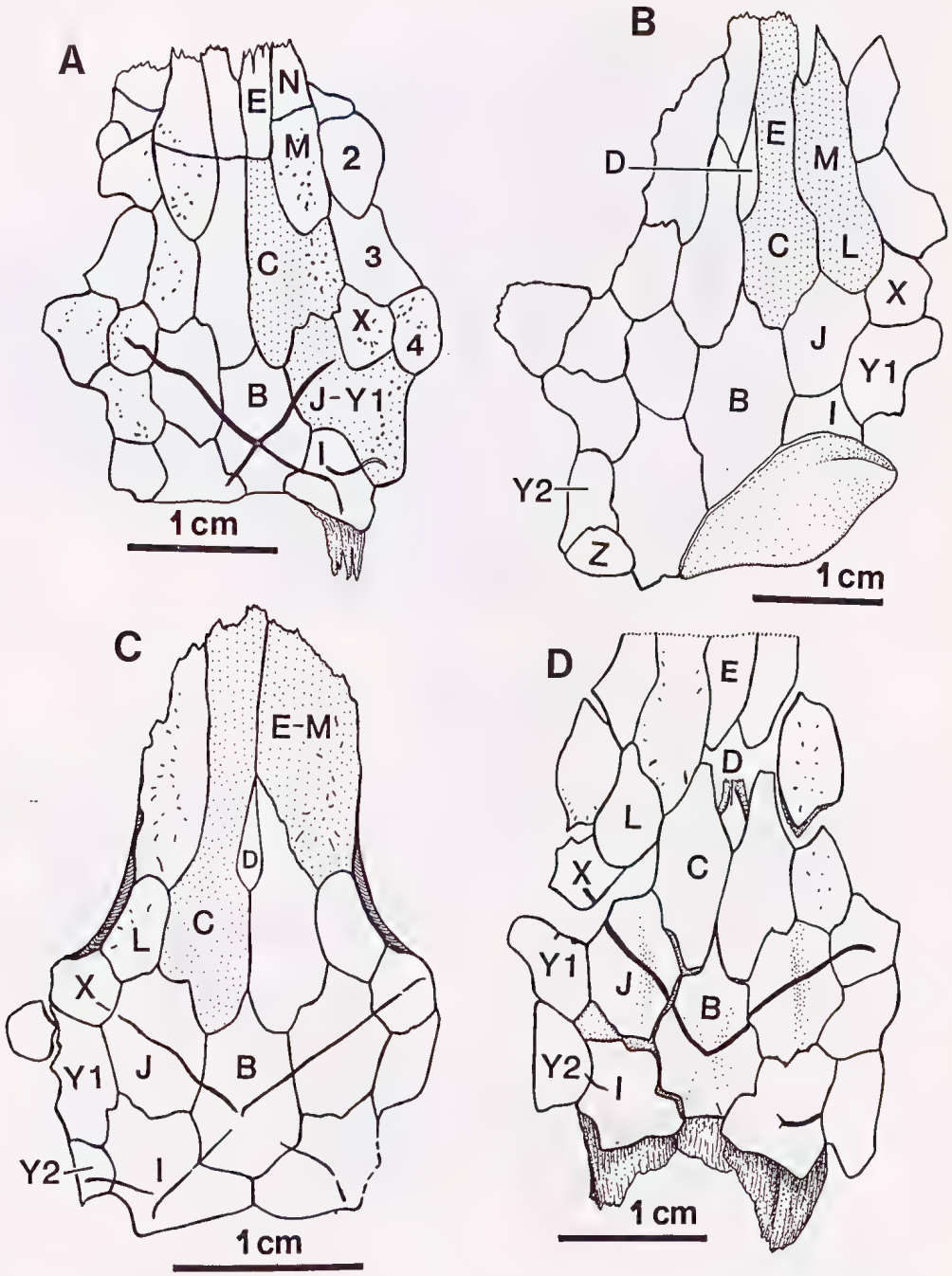

Fig.13. *Barwickia downunda* n.gen., n.sp., showing variations in skull roof patterns, with bone fusions shown as stippled areas. A, NMV P181786, dorsal view. B, NMV P181780, ventral view. C, WAM 90.7.1, dorsal view. D, NMV P181885, dorsal view.

anterior margin as in the E bones. The extrascapular bones comprise only Z-A-Z elements, with no evidence for G being present. Bone A is preserved *in situ* in a few specimens, suggesting it was loosely attached to the rest of the skull. In WAM 90.7.1 (Figs 12A, 15) it is shown as a robust quadrilateral bone deeply inserted into the skull roof, but in other specimens it is absent (WAM 90.7.7., Fig.13C).

Cheek. The pattern of cheek bones is quite variable and two variations are reconstructed in Figures 19B and C. The circumorbital bones are fewer in number than for *Howidipterus*. Bone 4 is larger and participates in more of the orbital margin than in the previous species. Bone O is always separately developed and large, with sometimes a smaller element anterior to it. As in *Fleurantia* (Graham-Smith & Westoll, 1937) the posteroventral, ventral and anteroventral margins of the orbit are bounded by only two bones, here designated 4 and 5 (Fig.19B), or combinations with 4+5 and 5+6 (Figs 14, 19C). Anterior to the very long and relatively thin 6+7 bone is a small but elongated 1a bone. The narrowness of these elements suggests that the skull of *Barwickia* was flatter anteriorly than in *Howidipterus*. Ventral to bone 4+5 in P181782 (Fig.14) there are five small elements, three of which are presumably bones 8, 9a, 9b and 9c, indicating extreme

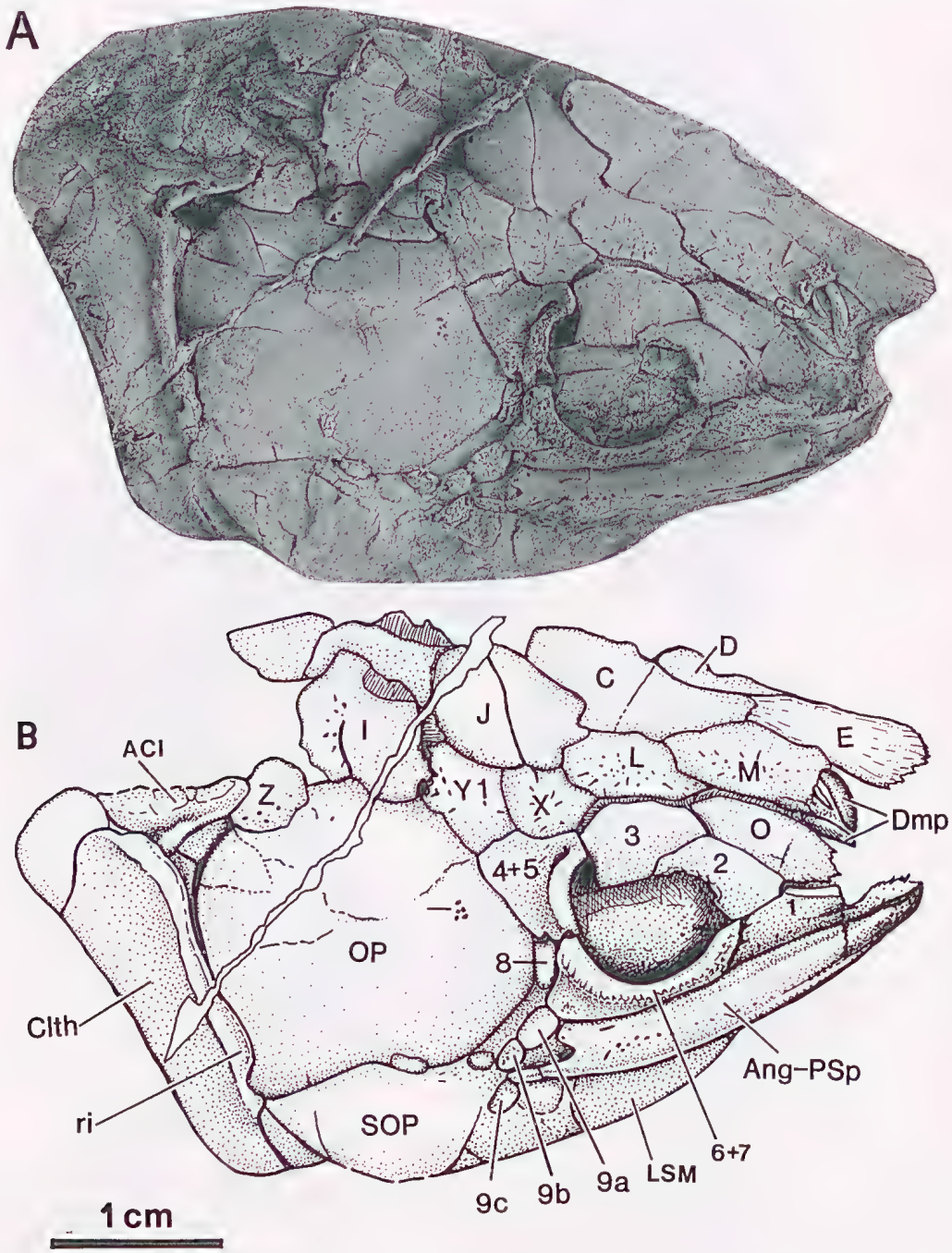

Fig.14. *Barwickia downunda* n.gen., n.sp., holotype specimen, NMV P181782, showing head in right lateral view.

reduction of these elements in *Barwickia*.

Sensory line system. The courses of the lateral line system in *Barwickia* are directly comparable with *Howidipterus*. Bone 3 sometimes has a short section of lateral line canal entering from bone 4, shown clearly by the visceral surface of P181780 (Fig.12B). The surface pit lines are not as deeply incised into the bones as those of *Howidipterus*. No pit lines are visible on bones 5, 6 or 8 in *Barwickia*.

Palate and dentition. The palate of *Barwickia* is well preserved in several specimens. Both P181780 and the holotype show the palate and part of the dentition (Figs 12E,F,G; 17). The parasphenoid (Fig.12E,F; restored in Fig.17) has a smooth buccal surface to the corpus with a well-defined buccohypophysial foramen. The stalk is slightly shorter, but much broader than for the previous species, terminating in an expanding region with a well-defined notch. It is grooved on the buccal surface. The pterygoids are composed of compact bone with radiating rows of large denticles with interspersed smaller denticles. The denticles are only found close to the lateral margins of the buccal surface of the pterygoids and prearticulars, not forming an extensive cover of denticles as occurs in *Griphognathus*, but similar to the condition in *Fleurantia*. There is no evidence of these tooth rows being formed on well-defined tooth-plate bases that attach to the pterygoid as in dipterids, and it is evident that *Barwickia* was a denticulate lungfish (*sensu* Campbell & Barwick 1986, 1990). This is seen not only from the morphology of the pterygoid and prearticular biting surfaces, but also in the fact that the hyoid arch is more strongly ossified than in *Howidipterus*, a condition better developed in the rasping feeders (e.g., *Uranolophus*, *Griphognathus*, Campbell & Barwick, 1983 1987, 1988).

Lower jaw. The lower jaw is poorly known from the material, and the course of the sensory line canals is only estimated from observation of pores in these few specimens. It is estimated to have been about 70% of the length of the skull roof. The combined angular plus postsplenial bone occupies most of the lower jaw length, forming most of the dorsolateral face of the lower jaw. Anterior to this long bone is a short, rather featureless splenial bone. In mesial view the angular + surangular bone bears a well-developed high preglenoid process (Fig.18C,D,E) as in other denticulate forms (e.g., Campbell & Barwick, 1986), with a well-rounded, narrow glenoid fossa. A small opening for the mandibularis V nerve is present just anterior to the preglenoid process (Fig.18B). Only small fragments on the prearticular are seen, and therefore the overall shape of this bone cannot be described. A small area of denticles is seen on the prearticular of P181890 (Fig.18A).

Operculogular bones. The operculogular series is poorly known apart from the operculum, as there is only one specimen showing part of the ventral surface of the head. The operculum is not as deep relative to its length as in *Howidipterus*. It is strongly

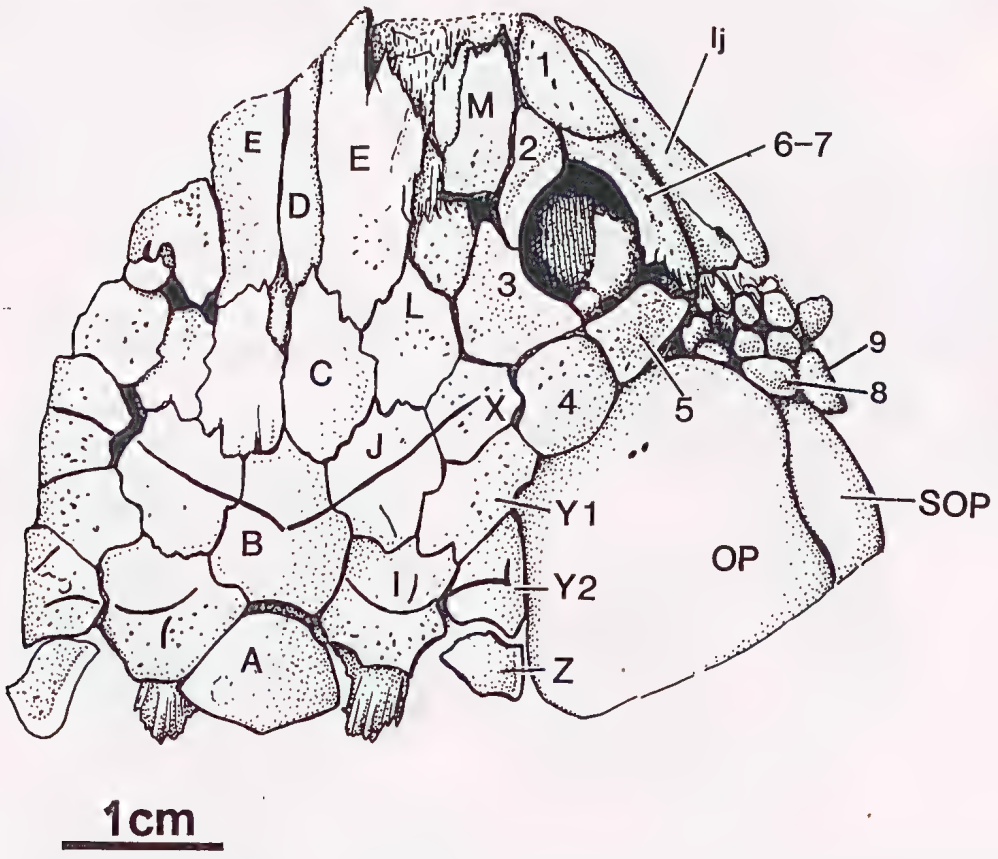

Fig.15. *Barwickia downunda* n.gen., n.sp., WAM 90.7.1., showing bones of the head in external view.

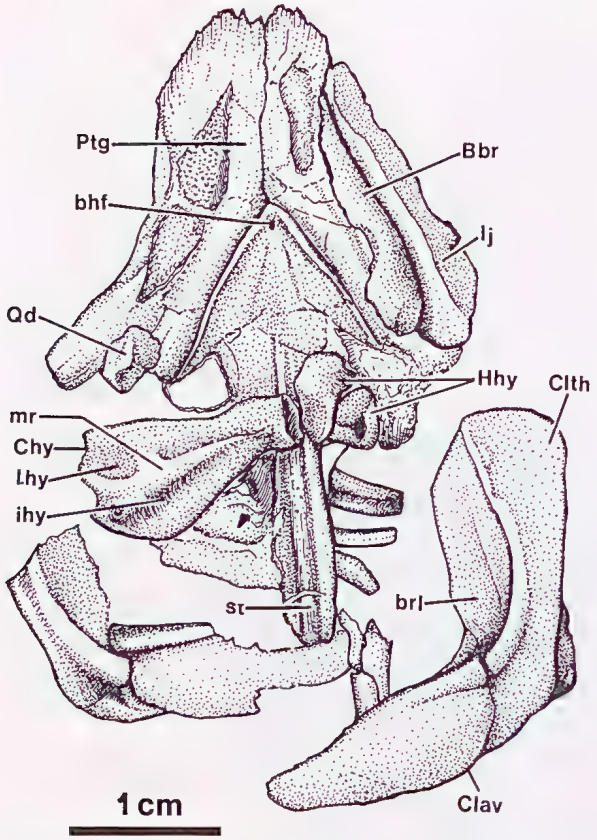

Fig.16. *Barwickia downunda* n.gen., n.sp., NMV P181868, showing parasphenoid and pterygoids in dorsal view, with elements of the visceral skeleton and shoulder girdle.

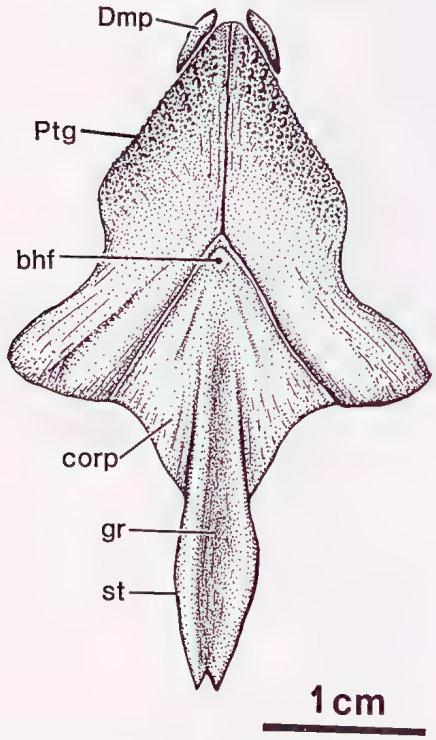

Fig.17. *Barwickia downunda* n.gen., n.sp., reconstruction of parasphenoid, pterygoid toothplates and vomers in ventral view, based on NMV P181780.

arched anterodorsally with an anteroventral projection reaching into the cheek to occupy the equivalent area that bones 8 and 9 occupy in *Howidipterus*. There is no scarred area on the visceral surface but there may be pits present on the external surface. Suboperculum 1 has not been positively identified, although in P181782 a bone below the operculum is probably this element. It is obscured dorsally by the operculum and ventrally by matrix, but indicates at least that it was greatly overlain by the operculum. Ventral to this bone and partially obscured by it is an element with a visceral surface exposed. It is oval and too large to be a posterior submandibular so it is probably a subopercular 2. P181890 shows a principal gular plate which is shaped similarly, and of comparable size to that bone in *Howidipterus*. The ventral operculogular bones of *Barwickia* need further investigation.

Visceral skeleton. The right ceratohyal is preserved in P181868 (Fig.16), and both ceratohyals, although poorly preserved, are seen in P181579. They are large bones, well ossified and about equal in size to the clavicle. It is of similar shape as the ceratohyal in other dipnoans (*Griphognathus*, *Chirodipterus*, *Uranolophus*, Miles, 1977; Campbell & Barwick, 1988). The lateral face bears a prominent crest running the full length of the bone and terminating posteriorly in a Y-shape.

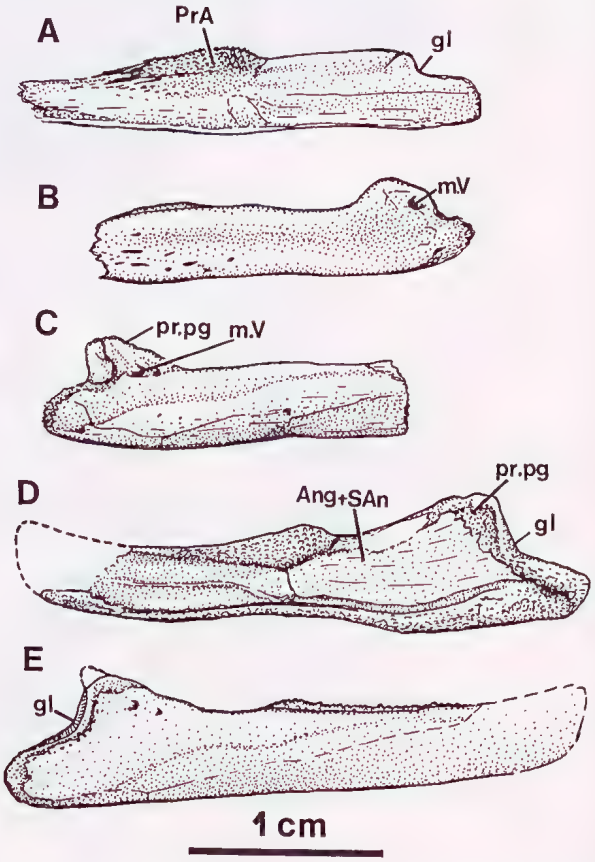

Fig.18. *Barwickia downunda* n.gen., n.sp., lower jaw bones. A, NMV P181890. B, WAM 90.7.1. C, NMV P181874. D, E composite restorations of the right ramus of the lower jaw in mesial (D) and lateral (E) views.

Anteriorly there is a pitted depression for the insertion of the levator hyoideus muscle, although it is smaller than for *Griphognathus*, being more similar in size to that in *Chirodipterus*. Ventral to the median crest about midway between the dorsal and ventral margins is a deep, slightly pitted groove for the insertion of the interhyoideus muscle. The mesial face of the ceratohyal is depressed along the centre and thin dorsally. Small foramina and grooves are evident close to the ventral margin near the weakly concave articulation surface for the hypohyal. There is no sign of a ventral notch as figured by Miles (1977, fig.136c) for *Griphognathus*. Overall the ceratohyal of *Barwickia* is more like that of *Griphognathus* than that of *Chirodipterus* in its flatter cross-sectional shape.

The hypohyal is also preserved in both specimens, associated with the ceratohyal. The ceratohyal and basibranchial articulation surfaces are tentatively identified, the latter being depressed, suggesting the bone was not completely ossified. P181869 shows traces of the left epibranchial elements, each being smaller then the element anterior to it. Little information can be obtained from these except that they were weakly ossified.

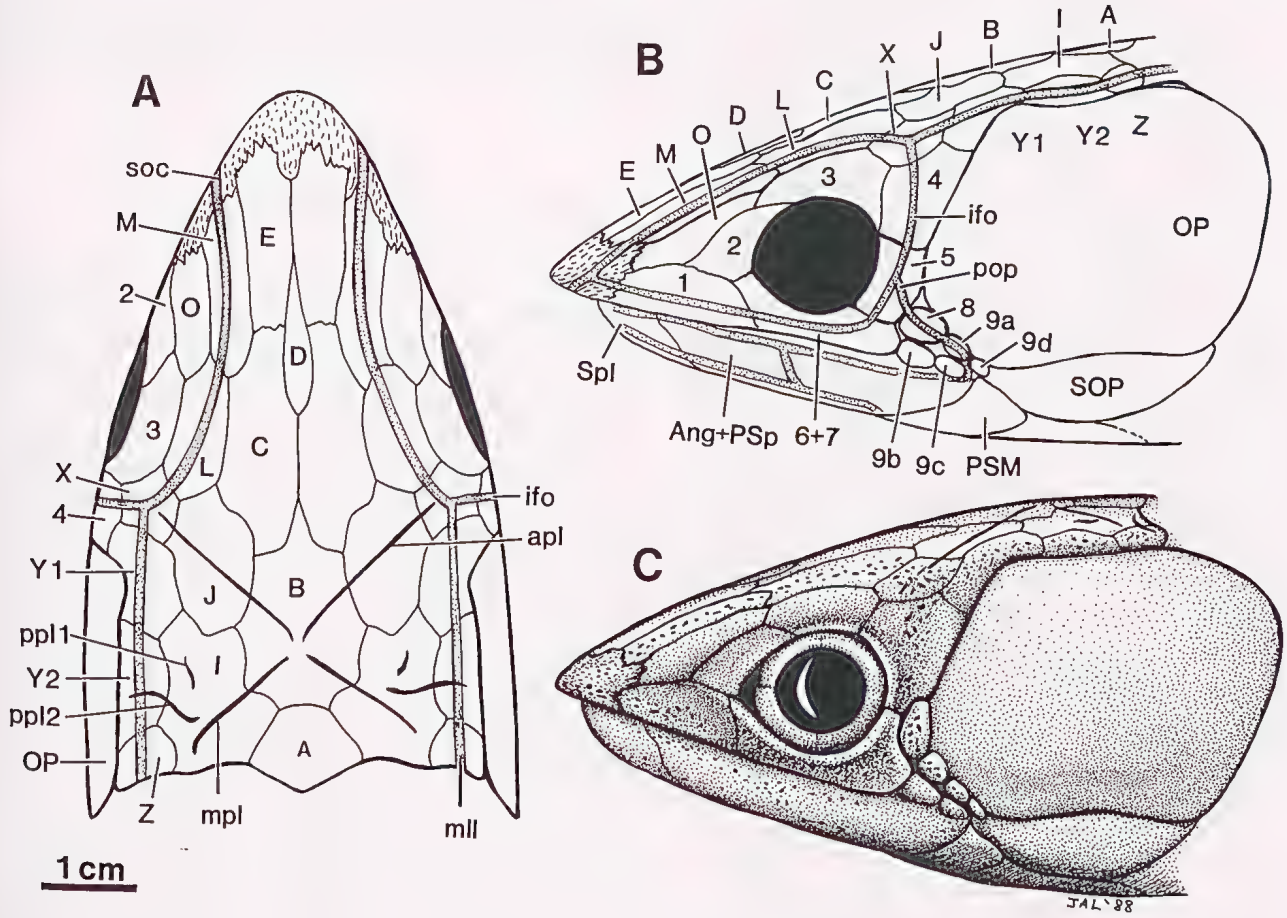

Fig.19. *Barwickia downunda* n.gen., n.sp., showing restoration of the head in dorsal (A) and lateral views (B, C). The two lateral views show variations in the infraorbital bones.

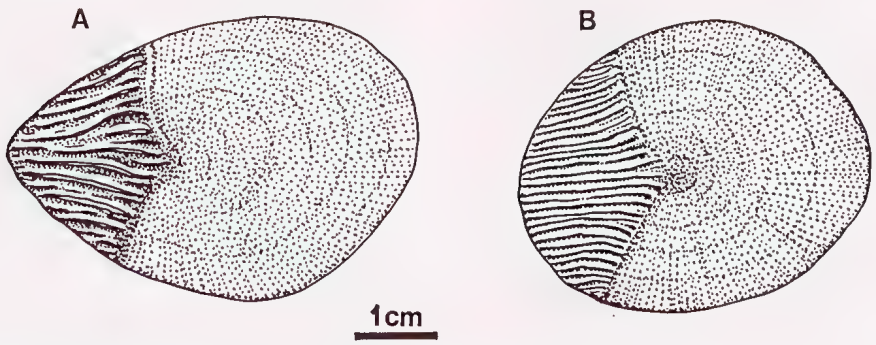

Fig.20. Composite reconstructions of the scales in external views of A, *Howidipterus donnae* n.gen., n.sp., and B, *Barwickia downunda* n.gen., n.sp. Bar scale = 1 mm.

Comparisons with Other East Gondwana Late Devonian Lungfishes

Few fossil lungfishes have been described from the East Gondwana region (incorporating Australia and Antarctica, Young, 1981) and the new genera can be easily distinguished from other contemporaneous forms, both described and undescribed material. The known forms include the marine Gogo fauna from Western Australia (Miles, 1977; Long, 1988b; Campbell & Barwick, 1990), *Eoctenodus* from Victoria (Long, 1987b), and various undescribed fragmentary remains from New South Wales and central Australia (e.g., Long & Turner, 1984). The Gogo Formation contains the chirodipterids *Chirodipterus* and *Pillararhynchus* (Miles, 1977; Campbell & Barwick 1990); the rhynchodipterid *Griphognathus* and the holodontid *Holodipterus*. These genera, because of their exquisite preservation, are readily distinguished from the new genera by their overall cranial shape and dentition. The *Soederberghia* skull described from the Cloghnan Shale of New South Wales (Campbell & Bell 1982) differs in its long snout and skull roof pattern.

Eoctenodus microsoma (Hills 1929) was originally described from fragmentary material from the Late Devonian Blue Hills Formation, near Taggerty, Victoria, by Hills (1929) but later referred to the European genus *Dipterus* (Hills, 1931). Long (1987b) redescribed the material and demonstrated that it differs from *Dipterus* by the shape of the parasphenoid and scales, thereby supporting Hills' original designation as a separate genus. *Eoctenodus* is known from well-preserved parasphenoid, pterygoid tooth plates, the cleithrum and isolated scales. In having true tooth plates it clearly differs from *Barwickia*. It differs from *Howidipterus* in the shape of the parasphenoid, which has a posteriorly broad corpus in *Eoctenodus*, and in the nature of the tooth plates, which have fewer tooth ridges in *Eoctenodus*, and even gradation of teeth along the ridges. In *Howidipterus* the tooth plates have well developed teeth near the margins, with mesially smooth and sparsely toothed areas. The scales of *Eoctenodus* and *Howidipterus* differ in that *Eoctenodus* scales have a more regular disposition of thin ridges over the external surface. The cleithrum is similar in its externally-exposed regions in both genera, but has a more extensive branchial lamina in *Eoctenodus*.

Young (1985, fig.8J) figured the skull of a lungfish (CPC 24697) from the Middle - Late Devonian Harajica Sandstone member of the Parkes Siltstone, central Australia. This specimen represents a short-headed fish which presumably lacks an ossified snout, has a large D bone, and retains a K bone in the skull roof. It resembles *Howidipterus* in the shape of the B bone, relative size of the C, D, I, and J bones, but differs in the larger number of bones laterally contacting C, and the smaller E bones (if complete in CPC 24697). It differs clearly from *Barwickia* n.gen. in the overall proportions, *Barwickia* having a longer, more slender roof pattern, and in particular the D bone is always thin and sliver-like, unlike that of CPC 24697.

The isolated dipnoan tooth plate from the Aztec Siltstone, Antarctica, figured by Campbell & Barwick (1987, fig.2), differs from the tooth plates of *Howidipterus* in having many teeth along each tooth ridge, and the mesial part of the plate has numerous cusps.

Isolated remains of Late Devonian lungfishes from the Hunter Siltstone, near Grenfell, New South Wales have been discussed by Long (1987b: 310-311). The parasphenoid of this undescribed dipnoan (Australian Museum F56323, F56155) clearly differs from both *Barwickia* and *Howidipterus* in having a very long stalk relative to the size of the corpus (30-37% total length). The associated tooth plates from the same locality differ from *Howidipterus* in having teeth along the entire tooth-ridge and in the fewer numbers of tooth ridges.

Comparisons with *Scaumenacia* and *Fleurantia*

The two new genera from Mount Howitt show close similarities to two genera from the contemporaneous Escuminac Formation of Quebec, Canada. To avoid further confusions some clear differences are listed here, but this list will require additional features of the postcranial skeleton when it has been described.

Howidipterus has cranial resemblances to *Scaumenacia*, but differs in the shape of the body and fins as it has a well-developed anterior dorsal fin, unlike the low, elongate anterior dorsal fin of *Scaumenacia*. The skull roof and cheek of *Scaumenacia* were described by Stensiö (1947) and Westoll (1949), and recent studies by Richard Cloutier, when published, will show further details of the cranial anatomy. The skull of *Howidipterus* can be distinguished from *Scaumenacia* by, *inter alia*, (i) having a D-bone always present, except when incorporated by fusion into the E bones, (generally, but not always, absent in *Scaumenacia*), (ii) the narrower B bone which has a well-defined anterior point (iii) the presence of paired rostral bones anterior to the E bones, (iv) the C bones are longer than the E bones, (v) the cheek has several small bones anterior to the orbit rather than a single large fused bone (this may not always be the case in *Scaumenacia* but is shown in Stensiö's reconstruction). The dentition is superficially similar in both genera but *Howidipterus* may have up to 17 tooth rows.

Barwickia has close resemblances to *Fleurantia* in its body and fin shape, but preliminary observation of its postcranial skeleton shows that the number of body ribs (vis. myotomal segments) is different, as is the number of fin basals in the anal fin (3 in *Fleurantia*, 4 in *Barwickia*). The skull of *Barwickia* differs in (i) its shorter snout shape, (ii) fewer supraorbital sensory line bones anterior to X, (iii) large A bone present, (iv) lack of a large single fused bone covering the dorsal surface of the snout. The differing shapes of the head in dorsal view also reflect the width of the pterygoids and parasphenoids –

much longer and narrower in *Fleurantia* than for *Barwickia*.

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APPENDIX

Abbreviations used in the figures

ACl	anocleithrum
Ang-SAn	combined angular + surangular bone
Ar	articular bone
Bbr	basibranchial
bhf	buccohypophysial foramen
brl	branchial lamina of shoulder girdle
Chy	ceratohyal
Clav	clavicle
Clth	cleithrum
corp	corpus of parasphenoid
Dmp	dermopalatine bones
gr	groove of parasphenoid
Hhy	hypohyal bones
ihy	attachment site for interhyoideus muscle
int V	foramen for mandibularis internis V nerve
LGul	lateral gular plate
l.hy	attachment site for levator hyoideus muscle
lj	lower jaw
LSM	lateral submandibular bone
mc	mandibular sensory line canal
MGul	median gular plate
mll	main lateral line canal
mpl	middle pit line groove
mr	median ridge on ceratohyal
m.V	foramen for mandibularis V nerve
LSM	lateral submandibular
mk.f	fossa for adductor mandibularis muscles
MSM	median submandibular
occ	occipital sensory line canal
OP	operculum
orc	oral sensory line canal
pits	surficial pits in operculum
plLG	lateral gular pit line
plMG	median gular pit line groove
pop	preopercular sensory line canal
ppl1,2	posterior pit line grooves
PrA	prearticular bone
pr.pg	preglenoid process on lower jaw
PSM	posterolateral submandibular bone
PSp	postsplenial bone
PT	post-temporal bone
Ptg	pterygoid tooth plate
Qd	quadrate
ri	ridge on cleithrum
Ros	rostral bone
SAn	surangular bone
soc	supratemporal sensory line canal
SOP	suboperculum
Spl	splenial bone
st	stalk of parasphenoid
Vom	vomer
vmp	foramen for efferent epibranchial artery

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The Sinolepidae, a Family of Antiarchs (Placoderm Fishes) from the Devonian of South China and Eastern Australia

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Abstract. Two new antiarchs are described, from the Late Devonian Hunter Siltstone near Grenfell in south-eastern Australia (*Grenfellaspis branagani* n.gen., n.sp.), and from the Early - Middle Devonian Dayaoshan Group in Guangxi, south-eastern China (*Dayaoshania youngi* n.gen., n.sp.). New material is described of *Xichonolepis qujingensis* P'an & Wang, 1978 from the Middle Devonian of Yunnan, and new interpretations are presented for *Sinolepis* Liu & P'an, 1958 from the Late Devonian of Jiangsu. All four genera are placed in the family Sinolepidae Liu & P'an, of which the most obvious defining character is the much reduced ventral laminae of the anterior and posterior ventrolateral plates of the trunk armour, and the presumed absence of a median ventral plate. Emended diagnoses are presented for the family Sinolepidae and the genera *Xichonolepis* and *Sinolepis*. It is suggested that *Grenfellaspis* and *Sinolepis* are immediately related, and the biostratigraphic, biogeographic, and palaeogeographic implications of this relationship are discussed. The vertebrate fauna from the Hunter Siltstone is regarded as the youngest nonmarine vertebrate horizon known from the Devonian of south-eastern Australia. A close palaeogeographic connection between south-eastern Australia and South and North China is indicated for the latest Devonian and earliest Carboniferous (late Famennian-early Tournaisian), which contrasts with the distinctive Devonian vertebrate faunas from the two regions in earlier strata. Other Devonian fossil groups showing a similar biogeographic pattern are considered in the context of competing hypotheses concerning the palaeogeographic relationships of Gondwana and Asia during the Middle Palaeozoic.

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The group of primitive fishes dealt with here first became known when Liu & P'an (1958) described some unusual antiarch remains from the Late Devonian Wutung Series near Nanjing (Fig.1, loc.2) as two new species in a new genus, *Sinolepis* Liu & P'an, which they referred to its own family, the Sinolepidae. This important paper provided the first indication of the highly endemic character of the early vertebrate fauna from the Devonian of China. Preliminary descriptions of other endemic groups soon followed (Early Devonian antiarchs, and galeaspid agnathans by Liu, 1963, 1965), and since then many publications have established the Devonian vertebrate fauna from South China as of central importance in understanding the early evolution of most of the major groups of Devonian agnathan and gnathostome fishes (for a recent review of the Devonian vertebrates of China see Pan & Dineley, 1988).

Gross (1965) was the first western scientist to attempt to incorporate *Sinolepis* into a general classification of the antiarchs. Gross divided the antiarchs into two major subgroups of ordinal rank, the Asterolepiformes and the Bothriolepiformes. He noted that the broad lateral plate of the skull in *Sinolepis* suggested bothriolepid affinity, and that the rectangular shape of the anterior median dorsal plate was reminiscent of the bothriolepid *Grossilepis*, but that the anterior median dorsal overlap relations, and the shape of the premedian, postmarginal, and opercular plates in the skull, were more similar to those of asterolepid antiarchs. Accordingly he placed the family Sinolepididae within his order Asterolepiformes. Miles (1968) followed this opinion, but Hemmings (1978) removed *Sinolepis* to the bothriolepididoids because of apparent similarities in pectoral fin structure. The distinctiveness of *Sinolepis* was recognised in the classification of Denison (1978), who divided the antiarchs into three major groups of equal rank, the Bothriolepidae, the Asterolepidae, and the Sinolepidae.

In Australia the discovery of sinolepid remains resulted from an investigation by AR in 1972 of a new fish locality in the Upper Devonian Hunter Siltstone near Grenfell in east central New South Wales (Fig.2A). The arthrodire *Groenlandaspis* from this locality was reported by Ritchie (1975), but a diverse associated fauna was also recovered, including remains of other placoderms, dipnoans, crossopterygians, and acanthodians. The placoderm material included bones belonging to the antiarchs *Bothriolepis* and *Remigolepis* (Ritchie, 1975), as well as other isolated plates with a distinctive tubercular ornament, which could be identified by their internal structure to be median dorsal plates from the trunk armour of an unknown antiarch. They resembled both *Sinolepis* and *Grossilepis* in the somewhat rectangular shape of the anterior and posterior median dorsal plates. But the most unusual bones were the ventral plates of the trunk armour, which in other antiarchs always have an extensive ventral lamina forming a complete ventral wall to the trunk armour. In this new antiarch the ventral lamina on both the anterior and posterior ventrolateral plates was reduced to two narrow strips running transversely and longitudinally along the ventral wall.

Photographs of these very distinctive bones were taken by GY to China in 1981. During discussions with Chinese colleagues Pan Jiang and Zhang Guorui in

Beijing, and examination of antiarch material held in the Institute of Vertebrate Paleontology and Paleoanthropology, and the Museum of Geology, it became clear that similar features were present in the ventral wall of the trunk armour in two Chinese genera, *Sinolepis* Liu & P'an, and *Xichonolepis* P'an & Wang. *Xichonolepis qujingensis* was erected by P'an & Wang (1978) for a few distinctive antiarch bones from the Middle Devonian of Yunnan Province, which they provisionally referred to the Bothriolepidae. Zhang (1980) described additional material, but concluded that *Xichonolepis* was an asterolepid antiarch. Young (1981, fig.5) proposed a scheme of antiarch interrelationships in which sinolepids were placed as the sister group of bothriolepiforms and asterolepiforms, with the Early Devonian yunnanolepids as the plesiomorphic sister

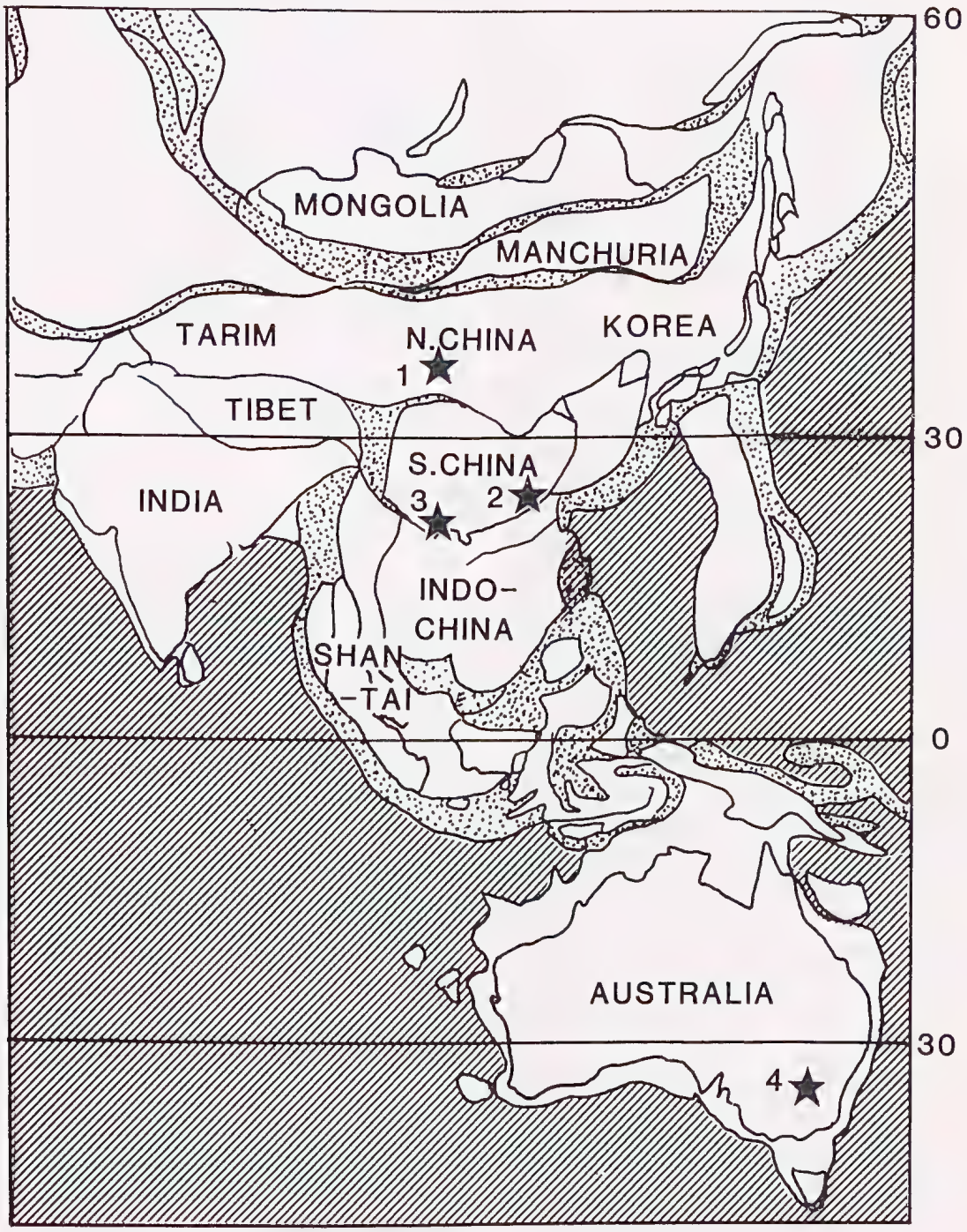

Fig.1. Distribution of Devonian Sinolepidae (Antiarchi). 1 - Ningxia Province, North China block (*Sinolepis*); 2 - Nanjing region (*Sinolepis*); 3 - Yunnan-Guangxi region (*Xichonolepis*, *Dayaoshania*, *Liujiangolepis*) and north Vietnam (*Vanchienolepis*; see Tong-Dzuy & Janvier, 1990), South China block; 4 - Grenfell region, Tasman Fold Belt, East Gondwana (*Grenfellaspis*). Modified from Scotese (1986) showing terranes comprising Asia and south-east Asia; *cf.* also Figure 35A,B.

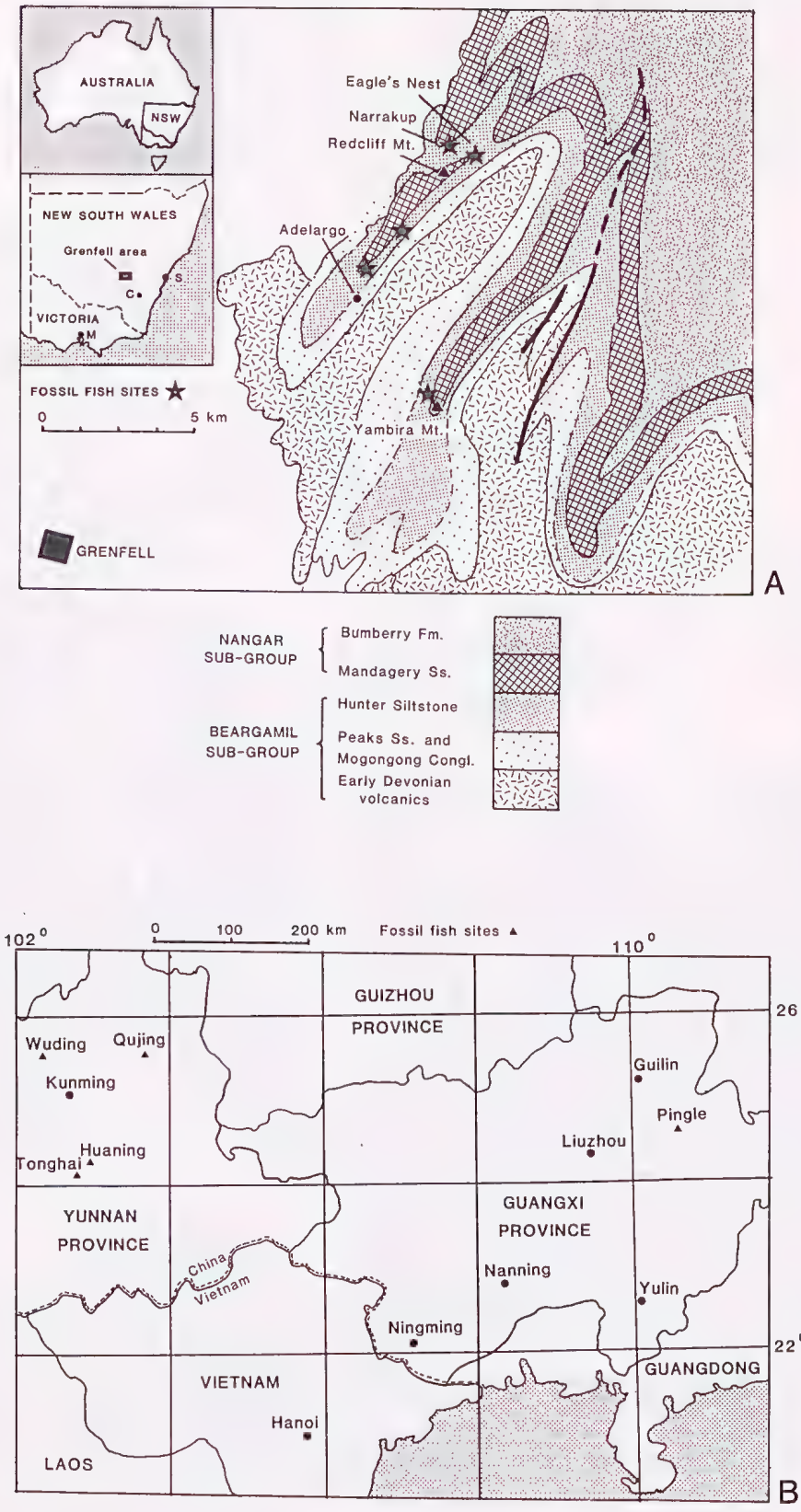

Fig.2. Sinolepid antiarch sites in Australia and South China. A - geological map of Grenfell area, eastern central NSW, Australia, showing Devonian succession (after Conolly 1965, fig.11) and fossil fish sites. S - Sydney; C - Canberra: M - Melbourne. B - sinolepid sites in Yunnan province (Wuding, Qujing, Huaning, Tonghai) and Guangxi province (Pingle), South China.

group to all remaining antiarchs. Janvier & P'an (1982) proposed a similar scheme, and distinguished non-yunnanolepids (sinolepids, bothriolepids, asterolepids) as a major group, the euantiarchs, characterised by a well developed brachial process. A similar opinion was expressed by Zhang (1979). They suggested that *Xichonolepis* may belong to the stem Bothriolepida, or that it may be the sister-taxon of the Bothriolepida. Long (1983) elevated the group to subordinal rank (the Sinolepidoidei), and tentatively included *Xichonolepis*, as did Young (1984c), who however suggested that sinolepids were the sister group of bothriolepidoids only.

It is evident that there has been considerable confusion as to the precise phyletic relationships of *Xichonolepis* and *Sinolepis*, and of the relationships of sinolepids as a group to other antiarchs, even though the distinctiveness of this group has been acknowledged since the initial descriptions of Liu & P'an (1958). Also of great interest are the biogeographic implications of the presence of a sinolepid in the Late Devonian of eastern Australia (see Young, 1981, 1984c, 1990a,b; Burrett *et al.*, 1990), this being the only occurrence outside of eastern Asia of an otherwise strictly endemic Chinese group. (A sinolepid recently reported from Vietnam by Tong-Dzuy & Janvier, 1990 comes from the southern edge of the South China Block).

The primary prerequisite to clarifying the phyletic relationships of sinolepids, and properly assessing their biogeographic implications, was seen to be an adequate description of the new Australian form. In this paper we describe this form as *Grenfellaspis branagani* n.gen., n.sp., and we describe another new form (*Dayaoshania youngi* n.gen., n.sp.) from material collected by Wang Shitao, Zhang Zhenxian and others in 1984. We complement these descriptions with an account of new material of *Xichonolepis* obtained since the earlier publications of 1978 and 1980, and we present emended diagnoses of *Xichonolepis* and *Sinolepis*, and provide a reinterpretation of the latter. These descriptions provide the background for a discussion of the interrelationships and relationships of sinolepids, and their biostratigraphy and biogeography. Higher classification of placoderms follows that of Denison (1978). The term 'Euantiarchi' is used in the sense of Janvier & Pan (1982) and Young (1984c). Throughout the text standard abbreviations are used for the dermal bones of antiarchs which mainly follow the terminology of Stensio (1948) and Miles (1968). Zhang (1984) has suggested new homologies for some of the bones of the antiarch pectoral fin, but for ease of comparison with earlier descriptions we use the older terminology here. Abbreviations for morphological structures used in the text and figures are listed in Appendix II. In the descriptions bone proportions are generally expressed as the ratio of length to breadth or breadth to length times 100 (abbreviated to B/L or L/B index). Bone measurements (Tables 1-6) are given in Appendix I.

Specimens described or discussed below are housed in various institutions, identified by prefix as follows: AMF – Australian Museum, Sydney; CPC – Commonwealth Palaeontological Collection, Australian Geological Survey Organisation, Canberra; IVF – Institute of Geology, Academy of Geological Sciences, Beijing; V – Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing; L, MGV – Museum of Geology, Ministry of Geology, Beijing.

Systematic Descriptions

Class **PLACODERMI**

Order **ANTIARCHI**

Suborder **SINOLEPIDOIDEI** Long, 1983

Sinolepidae Liu & P'an, 1958

Diagnosis. Orbital fenestra of head shield small; premedian plate wide, preorbital depression developed, triangular; postorbital division long; lateral plate large, wide, polygonal. Trunk armour low; dorsal wall slightly arched; ventral wall flat; ventral lamina of anterior and posterior ventrolateral plates greatly reduced, very narrow; median ventral plate absent and a large subrectangular ventral aperture present; ventrolateral margin of trunk armour developed as low ridge; prepectoral corners developed on ventral wall of trunk armour. Semilunar plates paired; subanal division short, posterior margin straight or concave. Anterior median dorsal overlaps anterior and posterior dorsolaterals; posterolateral margins of AMD short. Pectoral fin segmented, with flat articular processes on the dorsal and ventral central plates, no dorsomesial crest or mesial lamina on the dorsal central plate, a dorsal lamina on the first mesial marginal plate, and a small articulation on the first ventral central plate. Central sensory line groove, posterior oblique cephalic pit-line groove and posterior oblique abdominal pit line groove all absent.

Remarks. The defining characters of the suborder and family are discussed below in the section on sinolepid relationships.

Grenfellaspis n.gen.

Etymology. After the town of Grenfell, NSW, Australia, about 20 km from the type locality, and *aspis* (Gk), shield.

Diagnosis. Head shield small, broader than long, less than half as long as trunk armour; postpineal and nuchal plates do not overlap lateral plate; trunk armour long, narrow; processus obstans developed; anterior margin of AMD as broad as posterior margin. PMD lateral process not developed. Crista transversalis

interna posterior strongly developed, with the anterior margin of its median dorsal part united with the median ventral ridge; posterior ventral pit separate with posterior ventral process. AVL with one transverse crest on visceral surface; ventral wall of AVL and PVL straight, narrow, widest between prepectoral corners; semilunar plate(s) large; posterior marginal area of PMD well developed, bearing posterior ventral pit and process; ventral fossa articularis pectoralis small, shallow; axillary foramen small, triangular; pectoral fin slender, ventral area narrow, small and circular in shape. Boundary line between marginal and external articular areas not clear.

Remarks. The characters used to distinguish the new genus are discussed below in the section on sinolepid interrelationships.

Grenfellaspis branagani n.sp.

Figs 3-17

'undescribed form from eastern Australia' Young, 1981: 236, 237.
'antiarch from Grenfell' Long, 1983: 311.
'sinolepid nov.' Young, 1984c: fig.2.
'sinolepid nov.' Young, 1988a: fig.68.
'sinolepid' Young, 1990a: 247.
'sinolepid...from...near Grenfell' Burrett *et al.*, 1990: 168.
'new Australian genus' Young & Zhang, 1992: 448, fig.7C.

Type material. HOLOTYPE, AMF 78680, a left AVL in part and counterpart.

Other material. Head plates: PrM (AMF 54346, 56156, 56291, 78724, 79207, CPC 29102, 29103); PP (AMF 56295); Nu (AMF 56116, 56273, 56290, 56291, 56374, 78682, 78686, CPC 29105); L (AMF 56275, CPC 29106-29108); PNu (AMF 56346, 61457, 78681, CPC 29104, 29109). Trunk plates: AMD (AMF 56147, 56360, 56367, 56370, 61424, 61447, 78684, 78690, 78691, 78695, CPC 29110-29117); PMD (AMF 56136, 56136, 56174-5, 56282, 56292/56294, 56295, 56324, 56328, 56362, 56364, 56371, 78688, 78697, 78698, CPC 29118-29122); ADL (AMF 55308, 56146, 56148/56274, 56283, AMF 56295, 56363, 61438, 61433, 63891, 78682); PDL (AMF 56145, 56294, 61438, 78692, 78694, CPC 29123, 29125); AVL (AMF 56148, 56346, 61433, 61445, 61450, 78680, 78683, CPC 29126, 29127); PVL (AMF 55308, 56121-2, 56280-1, 56355-6, 56371/56374, 61451/56346, 78695, 78696, CPC 29128); Pectoral fin plates (AMF 56148/56274, 56280-1, 78693, CPC 29129-29131).

Type locality. Redcliff Mountain, about 20 km north-east of Grenfell, NSW (see Fig.1). Also collected from other localities in the vicinity (Mount Yambira, Narrakup, Eagle's Nest; Fig.2A).

Horizon. Hunter Siltstone of the Beargamil Sub-Group of the Hervey Group (Connolly, 1965).

Age. Late Late Devonian (late Famennian).

Etymology. After Dr David Branagan, Dept of Geology, University of Sydney, who drew the attention of A. Ritchie to this occurrence, and whose contributions to Australian geology are wide ranging.

Diagnosis. As for genus (only species).

Description. The material occurs as isolated bones scattered across bedding planes in a hard grey-green siltstone. Bedding planes are commonly completely covered with bone remains, mostly deeply weathered, which have been removed by etching in 20% hydrochloric acid, to allow casting with latex rubber of impressions. Much of the material is distorted, so estimates of proportions are only approximate. Strong distortion may be indicated by the elliptical shape of tubercles, but for moderate or slight distortion this is not a reliable criterion. For bilaterally symmetrical bones restoration of original shape has been carried out for selected examples using the techniques outlined by Ramsay & Huber (1983), and these have been used in preparing reconstructions of the whole armour (Figs 16,17).

Headshield. Of the bones from the headshield only the postmarginal has not been identified in the material. The premedian (PrM) plate (Fig.3E-J) is represented by six examples, each showing a triangular preorbital depression on the posterior division of the plate as in *Sinolepis* and *Xichonolepis* (see below), which takes the place of the preorbital recess of bothriolepid antiarchs. The PrM is broader than long (breadth/length index 162-217), and widest at the rostral margin, which is much wider than the orbital margin. The ornament continues to the rostral margin which is slightly convex. The posterior margin is occupied by the preorbital depression which reaches forward to the centre of the plate and is suggestive of Yunnanolepiformes. The depression is smaller than in *Yunnanolepis* and differs in that it does not reach the lateral plate. The lateral margins of the PrM are slightly convex, but less so than in *Sinolepis*.

In all specimens the infraorbital sensory canal groove can be clearly seen extending onto the plate from the middle of the lateral margin (ifc, Fig.5A). It forms a commissure (soc) in front of the preorbital depression. There is a strong ridge behind the sensory canal, but the left and right ridges do not meet in the midline. Two specimens show the visceral surface of the plate. In AMF 78724 the ventral surface of the preorbital depression is strongly convex (Fig.5B). A keyhole-shaped median depression, bordered by a ridge, extends anteriorly beyond the centre of the plate, and there is no sign of a premedian ridge and other structures seen in most other antiarch genera. CPC 29102 is similar but the median depression is relatively broader (Fig.3G). The ventrolateral margins of the PrM are vertical, and there is no ventrolateral notch.

There are four lateral (L) plates, each represented only by its dorsal impression (Fig.3A-D). The L was

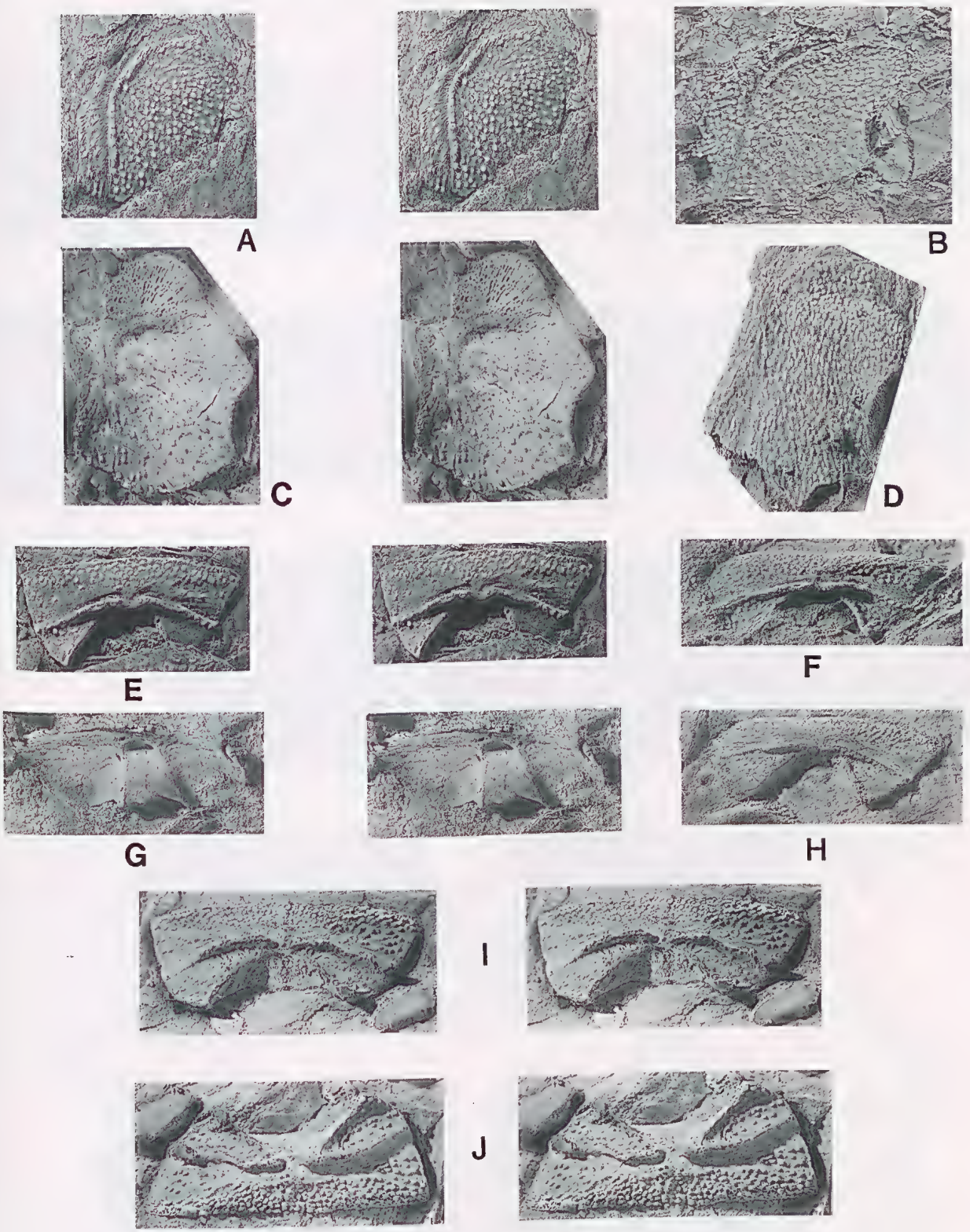

Fig.3. *Grenfellaspis branagani* n.gen., n.sp.; Hunter Siltstone, Late Devonian, near Grenfell, NSW, Australia. Premedian (PrM) and lateral (L) plates of headshield. Latex casts whitened with ammonium chloride. All specimens twice natural size (x2). A - left lateral plate, AMF.56275 (stereo pair); B - left lateral plate, AMF.78679; C - left lateral plate, CPC 29106 (stereo pair); D - left lateral plate, CPC 29107; E - premedian, AMF.56156 (stereo pair); F - premedian, AMF.79207; G-H - premedian, CPC 29102; G - ventral surface (stereo pair), H - dorsal surface; I - premedian, CPC 29103, dorsal view (stereo pair); J - premedian, CPC 29103, anterior view (stereo pair).

apparently a broad plate, the largest bone in the skull, and multilateral in shape. It was evidently similar to that of *Sinolepis* and *Yunnanolepis* in the very small orbital notch (Fig.5C), but details remain unclear. The orbital notch is only poorly preserved in the most complete specimen (CPC 29106, Fig.3C), and is missing from the

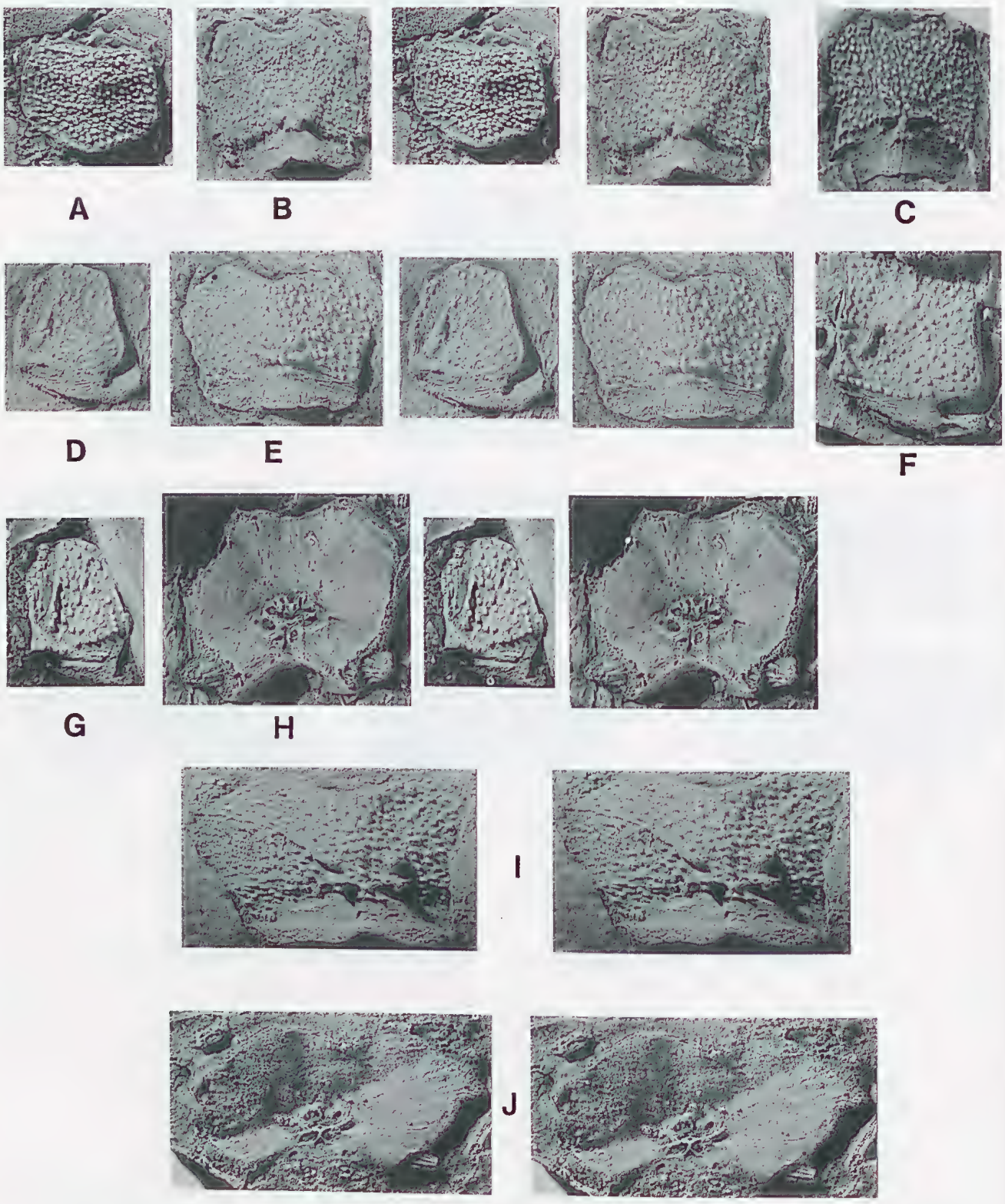

Fig.4. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Posterior and posterolateral plates of headshield. Latex casts whitened with ammonium chloride. All specimens twice natural size (x2). A - postpineal, AMF.56295 (stereo pair); B - nuchal, AMF.56273 (stereo pair); C - nuchal, AMF.78686; D - left paranuchal, AMF.79210 (stereo pair); E - nuchal, AMF.78682 (stereo pair); F - left paranuchal, CPC 29104; G - left paranuchal, AMF.78681 (stereo pair); H - nuchal (visceral surface), CPC 29105 (stereo pair); I-J - nuchal, AMF.78685 (stereo pairs: I - dorsal; J - ventral).

other examples. CPC 29106 is a nearly complete left plate (49.5 mm long, 36 mm wide; L/B index 138), which judging from tubercle shape has been somewhat distorted anteroposteriorly. It shows an expanded anterior part lacking ornament, and a distinct anterolateral notch (nprl, Fig.5C) not clearly preserved on other specimens. The orbital margin (om) is indicated as a notch on the ventral edge of the mesial margin, but the dorsal edge is straight so this was either abraded off or not developed. The anterior and lateral margins are convex. The anterolateral corner is indistinct, and the prelateral notch (nprl) as preserved in CPC 29106 is large (Fig.3C), but this is due to upward flattening of the margins. AMF 56275 and CPC 29107 show suggestions of a notch, but both are incomplete anteriorly. Behind the notch in CPC 29107 is a short pointed lateral process projecting downward. This specimen has a well-preserved lateral margin which thickens towards the posterior. The postmarginal contact is ill-defined immediately lateral to the sensory groove, and must have been small, even though the lateral division of the PNu is narrow. A slight notch mesial to the groove accommodated the anterior corner of the PNu. The Nu contact is straight in CPC 29106 but concave in CPC 29107, and the PP margin is concave in both. The orbital margin is short on the L plate, and the contact with the nuchal plate is oblique. It is clear that *Grenfellaspis* lacked the overlapping areas for the PP and Nu plates seen in *Sinolepis*. The infraorbital sensory groove (ifc) is near the lateral margin, with a strong ridge developed inside the groove as on the PrM. A shallow depression is variably developed behind the anteromesial section of the sensory groove. The bone is smooth with a few sparse tubercles lateral to the sensory groove in CPC 29106 and AMF 56275, but has normal ornament in CPC 29107 and 29108.

The postpineal (PP) plate is only known from one specimen, AMF 56295, a complete dorsal impression (Fig.4A). It differs from the PP of *Sinolepis* and Yunnanolepiformes in its slightly convex lateral margin, without overlap onto the L plate. Orientation of this specimen is based on the posterior margin, which is convex with a blunt medial angle corresponding to the shape of the postpineal notch on the Nu plate (Fig.4E). Compared with Nu plates of corresponding size, it was more than two thirds the length of the Nu plate. It is a subpentagonal plate (Fig.5D), and broader than long (L/B index 80). The anterior margin is straight to slightly concave.

The nuchal (Nu) plate is 'crown-shaped', and similar in outline to that of *Asterolepis* and *Pterichthyodes*, but

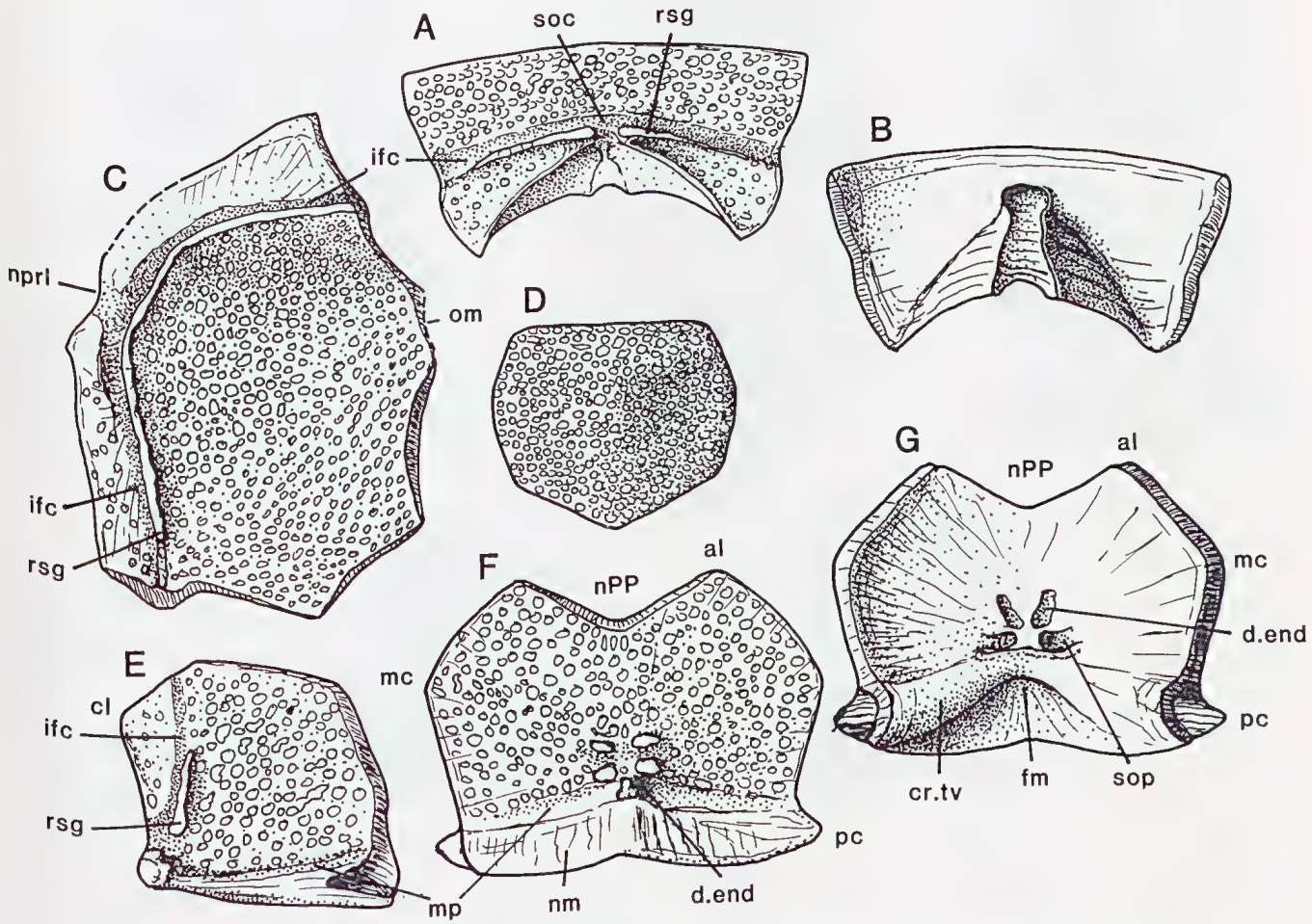

Fig.5. *Grenfellaspis branagani* n.gen, n.sp. Restoration of head plates: A,B - premedian (dorsal and ventral); C - left lateral; D - postpineal; E - paranuchal; F,G - nuchal (dorsal and ventral).

in its greater elongation it resembles the Nu of *Sinolepis* or *Yunnanolepis* (Fig.33C,D). The figured specimens (Fig. 4B,C,E,H-J) illustrate well the range of distortion in the material, with AMF 78686 elongated longitudinally, and 78685 elongated laterally. AMF 78682 and CPC 29105 appear relatively undistorted (based on ornament and intermediate proportions) and have been used for the restoration (Fig.5F). The L/B index is estimated at about 80 (measured range 76-105), based on the three best specimens (AMF 56157, 78582, CPC 29105).

The anterior division of the plate is shorter than the posterior division (Fig.5F). The anterolateral (al) and lateral corners (mc) are well developed, and the postpineal notch (nPP) is broad and shallow. The anterolateral margin is strongly oblique but the posterolateral margin tapers more gradually. The posterior margin is seen to be slightly concave in uncrushed specimens, which show the plate to be arched transversely at its posterior margin. Most specimens lack a posterior median process, but one is present in AMF 56290. The obtected nuchal area (nm) is not depressed far below the ornamented surface. The central sensory line groove is not developed, but part of the middle pit-line groove can be seen on AMF 78682 (Fig.4E) and other specimens (mp). Over the ossification centre of the plate there may be one (e.g., AMF 78682) or two (AMF 78685) pairs of enlarged tubercles, separating four shallow unornamented sulci, of which the posterior pair presumably represents the endolymphatic duct openings (d.end). However, no specimen shows a clear foramen here, and considering the detailed preservation of the material it seems that the duct may not have opened to the surface. The inner surface of the Nu (Figs 4H,J, 5G) shows two pairs of pits, as in other antiarchs, the anterior being the internal endolymphatic openings, and the posterior the supraoccipital pits (sop). The posterolateral corners (pc) are well developed and project beyond the lateral margins in AMF 56290, a large plate (20.5 mm across), and also the only one showing a posterior median process. AMF 78685 is the largest available Nu (28 mm across) but the posterolateral corners are obscured in external view. All other examples lack the posterolateral corners in external view (Fig.4B,C,E), but they are visible in specimens showing the visceral surface (Fig.4H,J), and fitted into a socket on the PNu. The visceral surface of the Nu plate, best seen in CPC 29105, shows a well developed transverse nuchal crista (cr.tv, Fig.5G), which forms a strong, anteriorly convex arc for the levator fossa (fm). The rounded contact margin across the crista for the PNu plate contrasts with the development of this area in *Bothriolepis* (e.g., Stensiö, 1948, fig.25), where the PNu forms a strong mesial process overlapped by the Nu. The posterior surface of the crista displays the well-developed fossa for insertion of the levator muscles of the headshield, but there is no median occipital crest.

The paranuchal (PNu) plate is represented by several almost complete examples (Fig.4D,F,G). It is a quadrilateral bone, as long as, or longer than, broad (L/B index 100, 120 in AMF 79210, 78681), with a convex anterior margin. The main difference in shape from the corresponding bone of *Bothriolepis* is the absence of the strong mesial process which underlies the transverse nuchal crista on the Nu plate in that form (see Stensiö, 1948, fig.27). The PNu is divided into a very narrow lateral division and wider mesial division by the infraorbital sensory canal groove (ifc, Fig.5E), which is a broad shallow groove as in *Sinolepis*. All available specimens show a short ridge of coalesced tubercles defining the mesial edge of the groove along its posterior half (rsg). Another shallow groove passing across the anterior edge of the obtected area may be the middle pitline (mp). At the posterolateral corner is a marked elevation of coalesced tubercles. The anteriorly situated lateral corner (cl) shows that the obstantic margin was more anterolaterally directed than in *Bothriolepis*. A marked notch and/or socket on the mesial margin received the posterolateral corner of the Nu.

No example of the postmarginal plate of *Grenfellaspis* has yet been located in the material, nor have any cheek plates (submarginal, suborbital, infragnathal) been identified.

Trunk shield. The bones of the trunk armour of *Grenfellaspis* are generally well represented, although as noted above no posterior lateral or median ventral plates have been found, and these are presumed to have been absent.

The anterior median dorsal (AMD) plate is strikingly long and narrow (Fig.6), with a B/L index ranging between 47 and 62 (Table 1), making it amongst the narrowest for known genera of Antiarchi. In some specimens (AMF 61447, 78684) both the dorsal and visceral surfaces are represented by complete impressions. The dorsal wall is slightly convex along the dorsal median line, but lacks a crest or median ridge. The tergal angle lies very close to the anterior margin of the plate and has an obliquely transverse depression. The lateral corner is not always distinct in dorsal view, but anterolateral and posterolateral margins are easily divided based on the overlapping areas seen on the visceral surface (Fig.6B,C).

The AMD is broadest posteriorly across the lateral corners. The anterior division of the plate is much longer than the posterior division (Table 1). The overlapping areas for adjacent bones are narrow. The anterior margin is straight, and about the same width as the posterior margin. The external postlevator process is weakly developed and situated near the anterolateral corner. The posterolateral margin of the plate is slightly arched. The posterior margin is concave, with a short posterior median process, and the overlap for the PMD restricted to the central part. Laterally the ornamented part of the AMD projected back to form a butt joint with the PMD.

On the visceral surface (Fig.6B,C,E) the postlevator thickening is strongly developed, but there is no

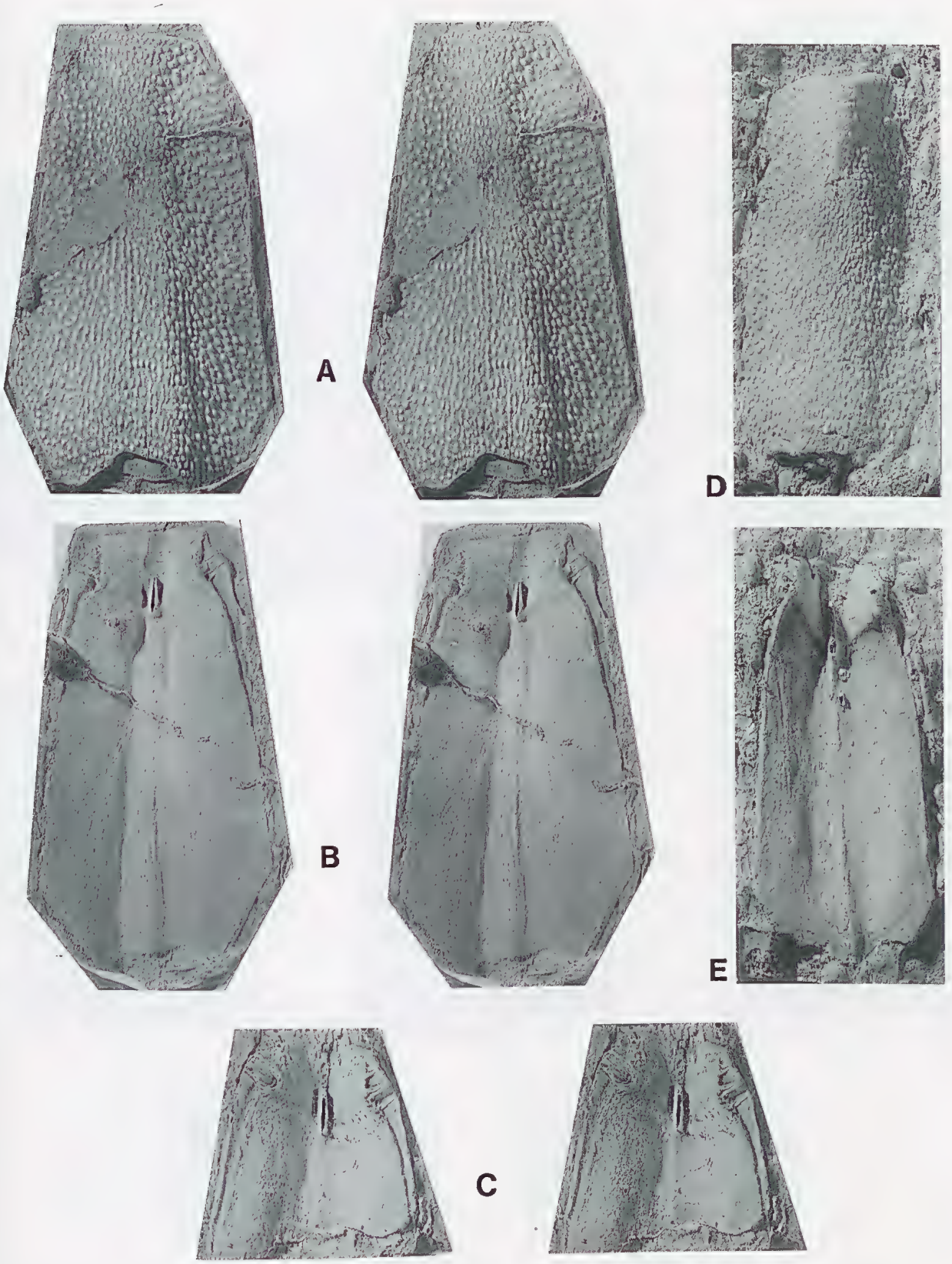

Fig.6. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Anterior median dorsal plates (AMD) of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A-B - anterior median dorsal, AMF.78684; A - dermal surface, B - visceral surface (stereo pairs); C - anterior median dorsal, AMF.56370, anterior part of visceral surface (stereo pair); D-E - anterior median dorsal, AMF.61447a,b; D - dermal surface, E - visceral surface.

postlevator crista. The levator fossa is short, about one sixth the length of the AMD. The anterior ventral process and pit are narrow and long, and situated at the posterior end of the levator fossa, between the posteromesial ends of the two postlevator thickenings. The ventral median ridge is strongly developed, and extends backwards from the anterior ventral process to the posterior margin.

The posterior median dorsal (PMD) plate is also long and narrow, and similar to the AMD in size and outline

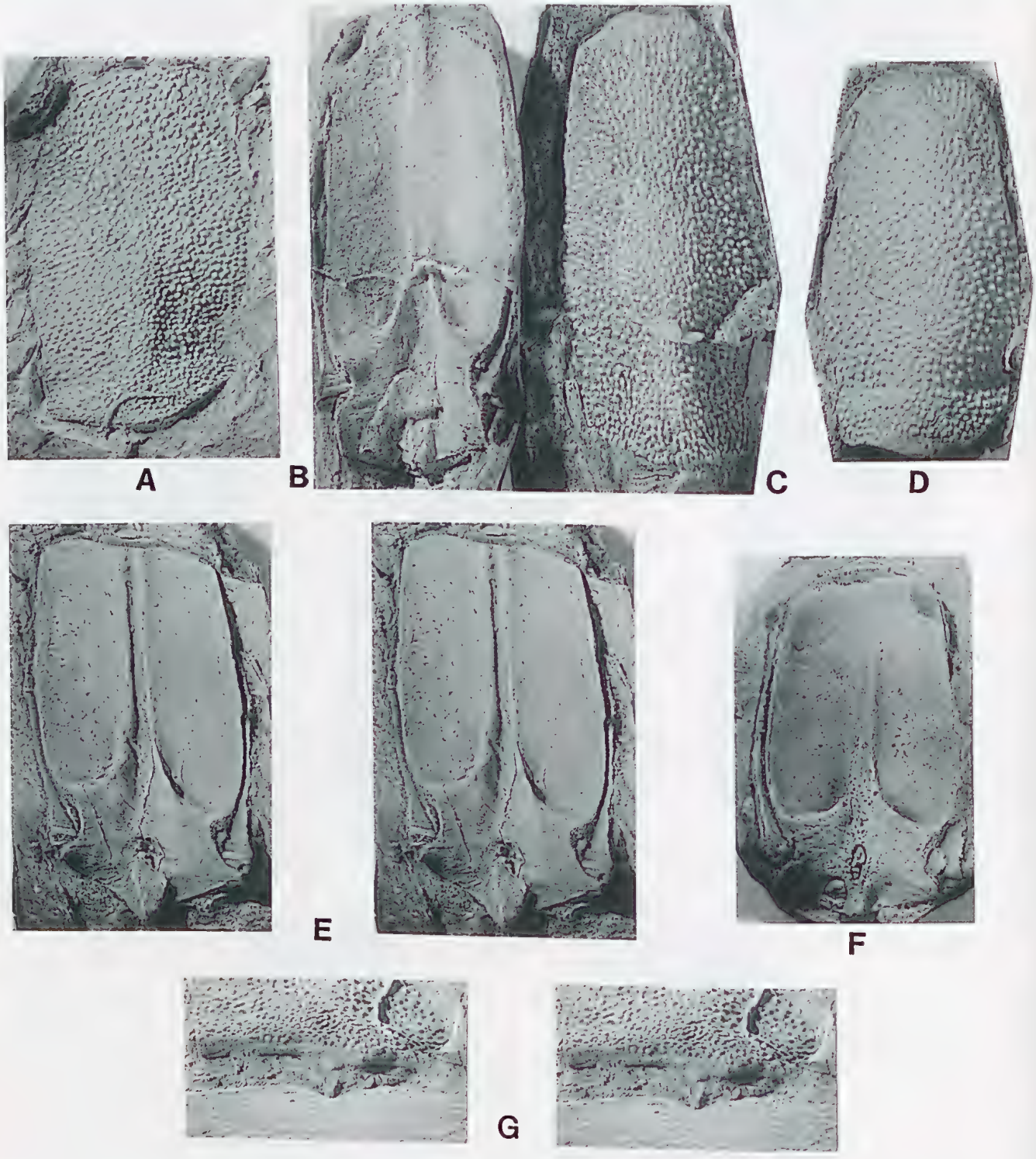

Fig.7. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Posterior median dorsal plates (PMD) of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A - posterior median dorsal, AMF.79203a; B-C - posterior median dorsal, AMF.56175; B - visceral surface, C - dermal surface; D - posterior median dorsal, AMF.56316; E - posterior median dorsal, AMF.79203b, visceral surface (stereo pair); F - posterior median dorsal, AMF.56324, visceral surface; G - posterior median dorsal, AMF.79202; posterior margin showing well-developed posterior process (stereo pair).

(Fig.7). In the most complete specimens (AMF 56136, 78678, 56294, 56328) the B/L index is between 43-55, but some examples are much more elongate (Table 2), possibly due to distortion. In shape the PMD compares with that of *Xichonolepis*, except in the absence of lateral processes (see below), which give it a quadrilateral shape. The anterior margin is strongly convex, but lacks an anterior angle. It is straight in the middle of this margin, as indicated also by the posterior margin of the AMD plate (e.g., AMF 56175, 78684). The long lateral margins are slightly convex, with narrow overlap areas in visceral view (Fig.7B,E,F). In contrast to *Xichonolepis* (see below) the lateral processes and corners are not well developed, and the plate is about the same width along its length. The posterior margin is rounded, but with a prominent angular median ventral process (Fig.7E-G), which is homologised with the posterior ventral process of the PMD in other antiarchs (see below).

On the visceral surface of the PMD the posterior internal transverse crista is very strongly developed, with a distinct anterior and rounded posterior margin (Fig.7E,F). The posterior marginal area takes the form of a paired shallow depression behind the crista on either side of the posterior ventral process, which projects back to the posterior margin of the bone. A prominent ventral median ridge with a ventral groove extends from the anterior margin of the PMD back to the posterior transverse crista, where it broadens to form the oblique anterolateral margin of the crista. The posterior ventral pit lies on the posterior part of the crista, and immediately in front of the posterior ventral process, situated entirely behind the crista. This arrangement differs from that of typical antiarchs (e.g., *Bothriolepis* or *Yunnanolepis*), in which the posterior marginal area is unpaired, and the posterior ventral pit and process lie in front of the transverse crista. However Zhang (1980) noted a similar arrangement in *Xichonolepis*, with both the posterior ventral pit and process lying behind the crista. The main difference between the two genera can be attributed to the slight development of the transverse crista in *Xichonolepis*, and correspondingly broader posterior marginal area (see below), such that both the pit and process lie behind the crista. In addition the pit and process are not separated as they are in *Grenfellaspis*.

The anterior dorsolateral (ADL) plate of *Grenfellaspis* is basically quadrilateral in shape (Fig.8A), but the absence of a well-developed dorsolateral ridge makes it difficult to distinguish the dorsal and lateral laminae. AMF 56148 is an almost complete but flattened ADL, with a B/L index of 60, but this value may be slightly high due to compression. In outline and proportions the *Grenfellaspis* ADL differs from that of both Bothriolepidae and Asterolepidae. The dorsal surface of the plate is widest anteriorly, and in dorsal view the anterior margin of the dorsal lamina is straight, with a convex obstantic process developed laterally. The mesial margin of the plate is slightly concave, reflecting the absence of a strong external postlevator process or postnuchal notch on the AMD. The posterior margin of the ADL is convex, with a posterior corner developed on the dorsal lamina. The lateral margin is convex anteriorly and straighter posteriorly. The well-developed lateral line groove is bordered dorsally by a prominent ridge of coalesced tubercles, as on the PNu, L, and PrM bones of the skull. The groove is broad and ill-defined laterally, grading into the narrow, depressed margin of the lateral lamina, which tends to be sparsely ornamented posteriorly (Fig.8C). The overlap area for the AVL plate is only developed at the anterior end (Fig. 8F). Whether or not there was contact with the PVL plate, as described below in *Dayaoshania* and *Xichonolepis*, is not clear in the available specimens.

As seen on AMF 56292 (Fig.8D-F) the crista transversalis interna anterior is strongly developed, with the articular fossa for the paranuchal trochlea of the headshield well displayed (Fig.8E). The fossa is bordered below by a well-developed infra-articular crest, but a supra-articular crest is absent.

The posterior dorsolateral (PDL) plate, like the ADL, is long and narrow (Fig.9). It is broadest across its dorsal corner, which is developed much as in *Xichonolepis*. Posteriorly the plate becomes gradually narrower, also as in *Xichonolepis*. As with the ADL the boundary between the dorsal and lateral laminae is not clear, the external surface of the plate being gently convex, without a dorsolateral ridge. One uncrushed specimen (CPC 29123) reveals that the lateral lamina is very low and of equal height throughout its length, as on the ADL. The ventral margin is straight and the main lateral line groove is clearly marked just inside the margin (Fig.9B,E). The posterior margin of the PDL is short and concave, and in visceral view shows a strongly developed crista transversalis interna posterior (Fig.9F,G).

The PDL is overlapped anteriorly by the ADL as in all other known antiarchs. Dorsomesially it is overlapped anteriorly along a short margin by the AMD, and posteriorly along a much longer margin by the PMD. CPC 29123 shows a strong buttress of cancellous bone which fitted against the strong transverse posterior thickening developed on the PMD as described above. The narrow overlap area on the ventral margin is only developed posteriorly, and is assumed to be for the PVL, because the low lateral wall provides no space for a separate posterior lateral plate, and no such element has been identified in the material.

The most unusual plate in the trunk armour of *Grenfellaspis* is the anterior ventrolateral (AVL) plate (Fig.10). The most complete example in the Australian Museum collection (AMF 78680, a left AVL) has been selected as the holotype of *Grenfellaspis branagani* n.gen., n.sp. It is preserved as an external and internal impression showing virtually all the features of this distinctive and definitive plate (Fig.11).

As in other Antiarchi the AVL of *Grenfellaspis* is made up of lateral and ventral laminae, but it differs strikingly from previously described antiarch genera in the very low lateral lamina, and the greatly reduced

posterior part of the ventral lamina, which has a deep, almost right-angular mesial embayment (m3, Fig.11). The holotype is 72 mm long and 28 mm wide anteriorly (L/B index 257), but behind the level of the brachial articulation the ventral lamina is reduced to only 7 mm wide, and posteriorly it narrows to 5 mm. The ventral lamina thus comprises a broad anterior subcephalic division comparable to that of other antiarchs, and an elongate narrow posterior division, which enclosed only the lateral side of the ventral surface of the trunk (Fig.17).

On the ventral lamina the subcephalic division has the anterolateral corner strongly developed (c.al, Fig.11), and there is a slight anteromesial corner (c.am) on the free anterior margin, which is concave and very short. The anterior division (m1) of the mesial margin is comparatively long and wide, forming a deep rectangular notch. Its shape is somewhat similar to that of the Early Devonian *Yunnanolepis*, but in *Grenfellaspis* it is much deeper, with its posterior margin level with the prepectoral corner (prc). The middle division (m2) which met the opposite (right) AVL is straight and very short (in the holotype 11 mm long, only about 16% of total length). A well-developed corner of the middle division was present on the right plate where it overlapped the left, as shown by the shape of the overlap area

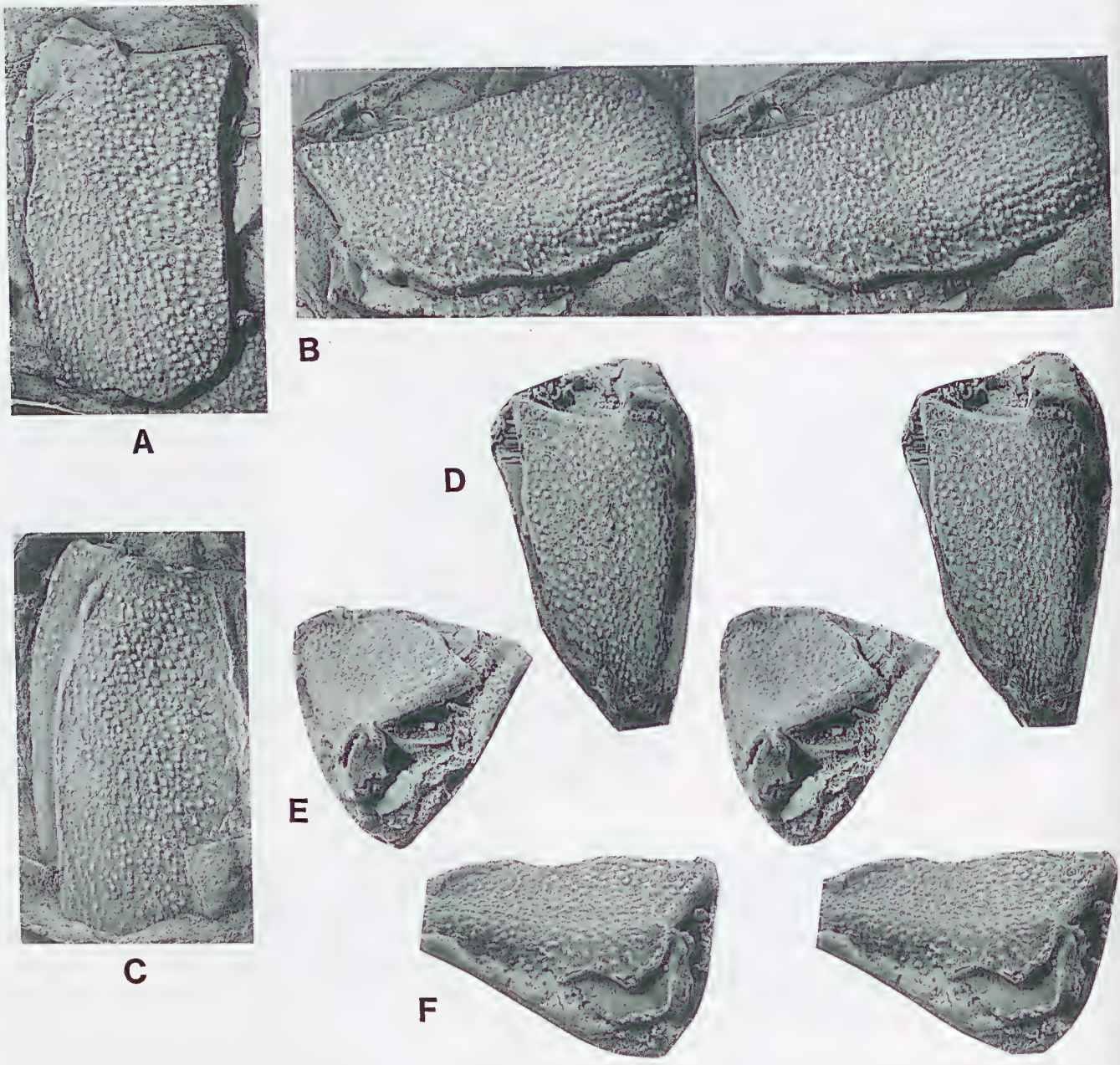

Fig.8. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Anterior dorsal lateral plates (ADL) of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A-B - left anterior dorsolateral, AMF.56148; A - dorsal view, B - oblique anterolateral view (stereo pair). C - left anterior dorsolateral, AMF.56295, dorsal view; D-F - right anterior dorsolateral, AMF.56292; D - dorsal view, E - anterior view, F - dorsolateral view (stereo pairs).

(oa.AVL), but the left plate has no corner developed. The posterior division (m3), corresponding to the margin with the median ventral plate in other antiarchs, is very specialised as a deep rectangular embayment. In the holotype it is 54 mm long (measured from corners c4 to c5).

The well-developed prepectoral corner (prc) is best preserved on AMF 61446. The AVL is broadest between this corner and the median contact between left and right plates. The subcephalic division is relatively shorter than in other known antiarchs. In the holotype it is about 13 mm long, and only 20% of the length of the plate.

The anterior margin of the lateral lamina is essentially

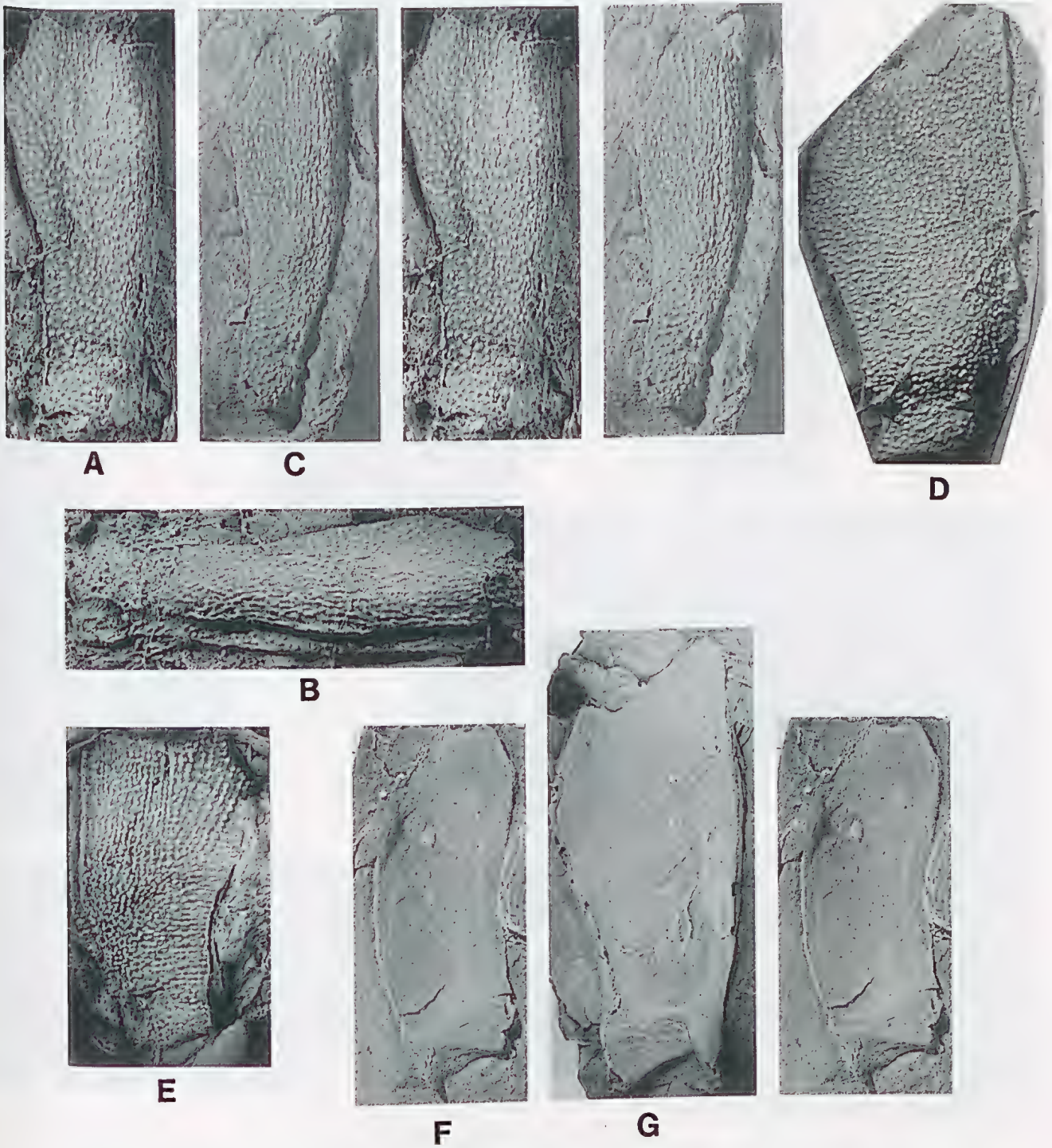

Fig.9. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Posterior dorsolateral plates (PDL) of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A-B - right posterior dorsolateral, CPC 29123. A - dorsal view (stereo pair), B - lateral view; C - right posterior dorsolateral, AMF.79208, dorsal view (stereo pair); D - right posterior dorsolateral, AMF.78694, dorsal view; E - left posterior dorsolateral, CPC 29124, dorsal view; F - right posterior dorsolateral, AMF.79209, visceral surface (stereo pair); G - left? posterior dorsolateral, AMF.61438, visceral surface.

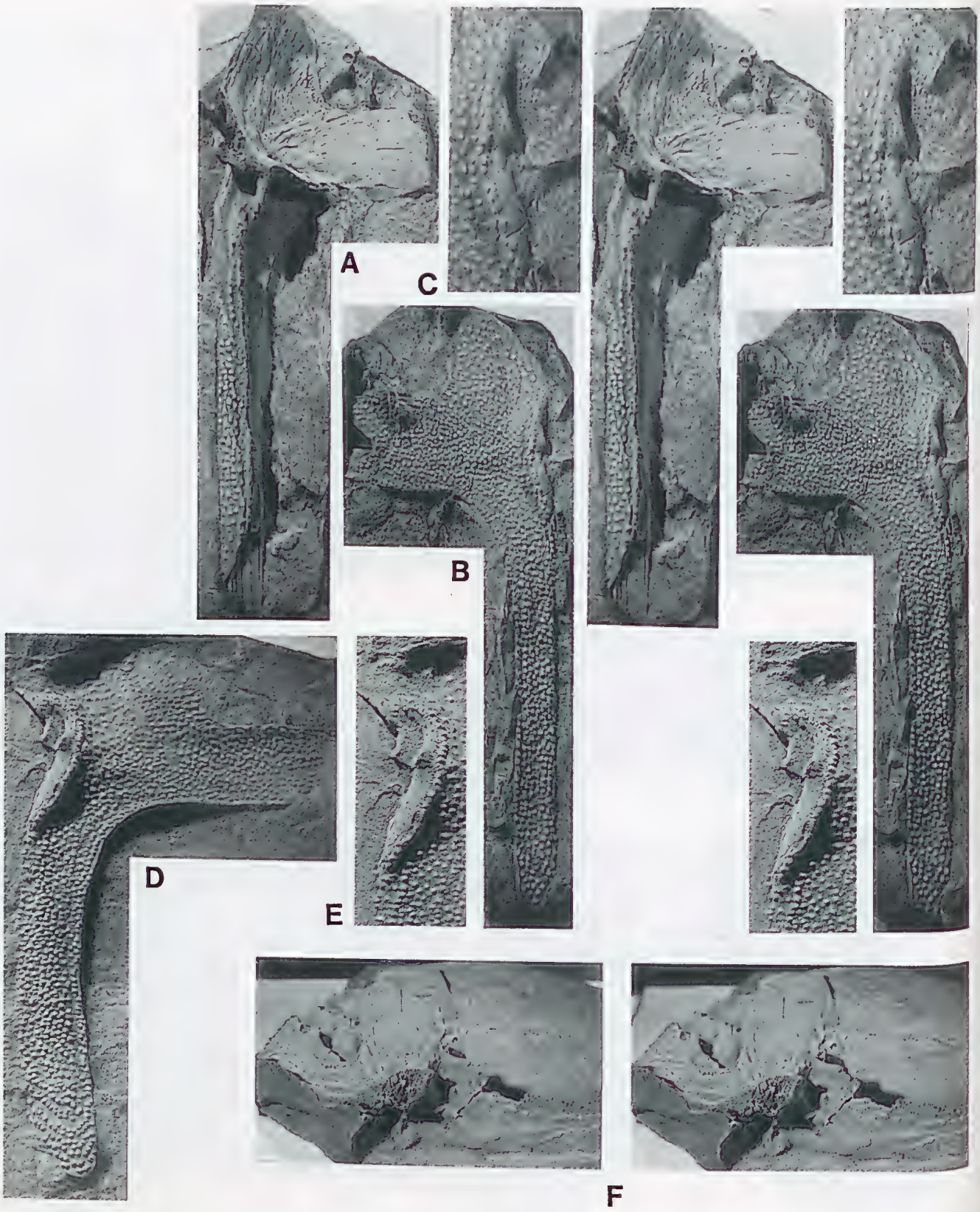

Fig.10. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Anterior ventrolateral plates (AVL) of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A-C,F - left anterior ventrolateral, AMF.78680 (HOLOTYPE); A - dorsal (visceral) view (stereo pair), B - ventral (dermal) view (stereo pair), C - detail of brachial region (stereo pair), F - dorsolateral view of brachial region in AMF.78680 (stereo pair). For interpretation *cf.* Fig.11A-C. D-E - right anterior ventrolateral, AMF.78683, ventral view; D - whole AVL, E - detail of brachial area (stereo pair).

as in other Antiarchi, passing ventrally from the dorsal corner (dc, Fig.11C) into the free lateral margin of the subcephalic division. The dorsal margin of the lateral lamina shows a somewhat more complex development than in other forms but the overlap relationship to the ADL is comparable. In front of the dorsal corner a triangular rugose articular area faces dorsolaterally (art.d, Fig.11C), separated by a narrow neck of ornamented bone from a groove (cf. ADL, Fig.11B). This groove runs down the inside of the dorsal corner onto the anterior transverse crista (cit2), which formed the anterior overlap onto the ADL. Posteriorly is a short section of rounded margin without overlap surfaces, behind which the straight dorsal margin carries a shallow groove

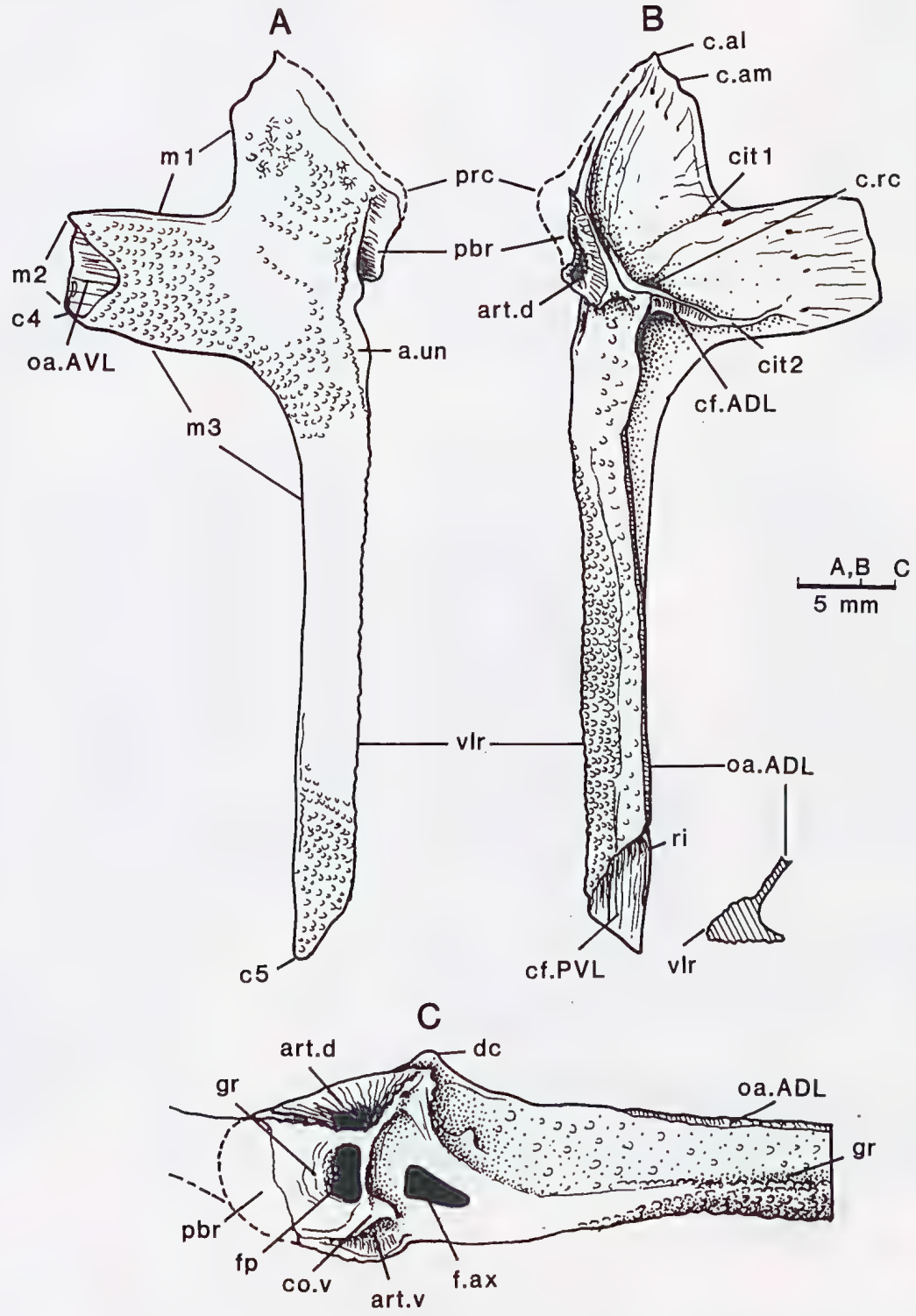

Fig.11. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Holotype, AMF.78680. Left anterior ventrolateral plate (AVL), *cf.* Fig.10A-C,F. A - ventral, B - dorsal (with cross-section at the level shown) and C - lateral views.

into which the ventral margin of the ADL abutted (oa.ADL). The external surface of the lateral lamina comprises a dorsolaterally facing ventral part with crowded tubercles (forming the rounded dorsal surface of a strong ventrolateral ridge or keel formed jointly by the ventral and lateral laminae), and a laterally facing dorsal part on which tubercles are sparse. The two regions are separated by a shallow groove (gr).

On the internal surface of the plate the main branch of the crista transversalis interna anterior is well developed (cit2). It is fairly high and sharp-edged, and decreases in height mesially to terminate before the midline, and does not join up with the crista on the opposite AVL. A weaker anterior branch of the crista transversalis (cit1) runs anteromesially from the inside of the dorsal corner straight to the posterolateral corner of the semilunar notch. Between the two branches a large foramen (c.rc) opens into a shallow groove running anteromesially behind the anterior branch of the crista, which corresponds presumably to the 'rostro-caudal canal' described by Stensiö (1931: 97).

In the midline the right AVL overlaps the left, and posteriorly the AVL overlaps the PVL, as in other antiarchs. The internal lateral margin of the semilunar notch displays an overlap area but the posterior division of the medial margin (m3, Fig.11) lacks any trace of an overlap. No example of a large rectangular median ventral plate required to fill this space has been identified in the abundant material recovered from several sites near Grenfell, and we suggest therefore that the median ventral plate was not developed in *Grenfellaspis*. Posteriorly the contact face for the PVL (cf. PVL) has its mesial margin delineated by a narrow ridge (ri), which is consistent with this suggestion.

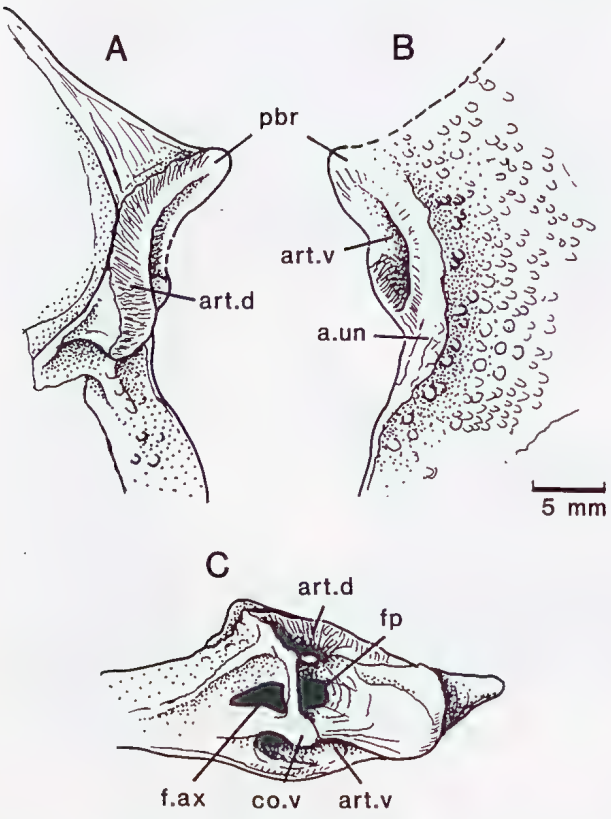

Fig.12. *Grenfellaspis branagani* n.gen, n.sp. Late Devonian, NSW, Australia. Right anterior ventrolateral plate, AMF.61445-6. Detail of brachial area in A - dorsal, B - ventral and C - right lateral view.

A rudimentary processus brachialis of unusual form (pbr) is incompletely preserved in the holotype, and clearly seen in ventral view (Fig.10B,C). Similar preservation is seen in AMF 61445 and 78683 (Figs 10D,E,12). In lateral view these specimens show the foramen axillare (f.ax) to be small and triangular in shape, with its long axis horizontal. A ventral fossa articularis pectoralis (art.v) of unusually small size is visible in lateral and ventral views immediately anteroventral to the axillary foramen. This small fossa is placed near the ventral margin and must have received the articular process of the first ventral central plate of the pectoral appendage described below (Figs 14,15). It lies beneath a thickened ventral part of a vertical lamina forming the posterior boundary of the funnel pit (fp). By comparison with the corresponding partition between the axillary foramen and funnel pit in *Bothriolepis* (e.g., Stensiö, 1948, fig.51A), this ventral thickening (co.v) must be a rudimentary ventral portion of the brachial process (ventral pars condyloidea). The triangular dorsal articular area mentioned above (art.d) must have received the articular process of the first dorsal central plate of the pectoral appendage described below, with the fin pivoting around a single axis passing through the dorsal and ventral articulations.

In the articulation of the pectoral fin *Grenfellaspis* thus differed markedly from more advanced antiarchs with a large helmet-shaped processus brachialis, such as *Bothriolepis*, *Asterolepis* and *Remigolepis*. In these forms the dorsal and ventral articulations are deep hemispherical grooves separated anteriorly by the narrow pars pedalis of the brachial process. In *Grenfellaspis* however, as far as can be determined, there was no pars pedalis, the anterior edge of the brachial process being continuous with the prepectoral corner of the AVL (best seen in AMF 61445, 61446; Fig.12). The ventral position of the ventral articular fossa is reminiscent of the brachial articulation in *Hyrcanaspis bliecki* from the Middle Devonian of Iran (Janvier & Pan, 1982), but that form also had a large normally developed brachial process. Similar discrete dorsal and ventral articulations are seen in the brachial fossa of *Procondylolepis* (Zhang, 1984), but they differ in being closer together and in front of the funnel pit. In *Grenfellaspis* the articular areas of the pectoral fin are more widely separated, lying above, below and slightly behind the funnel pit. This implies a high proximal brachial aperture to the fin, of the type seen in advanced antiarchs (abp, Stensiö, 1948, fig.196).

The posterior ventrolateral (PVL) plate superficially resembles the AVL, but in reverse (Fig.13). The PVL

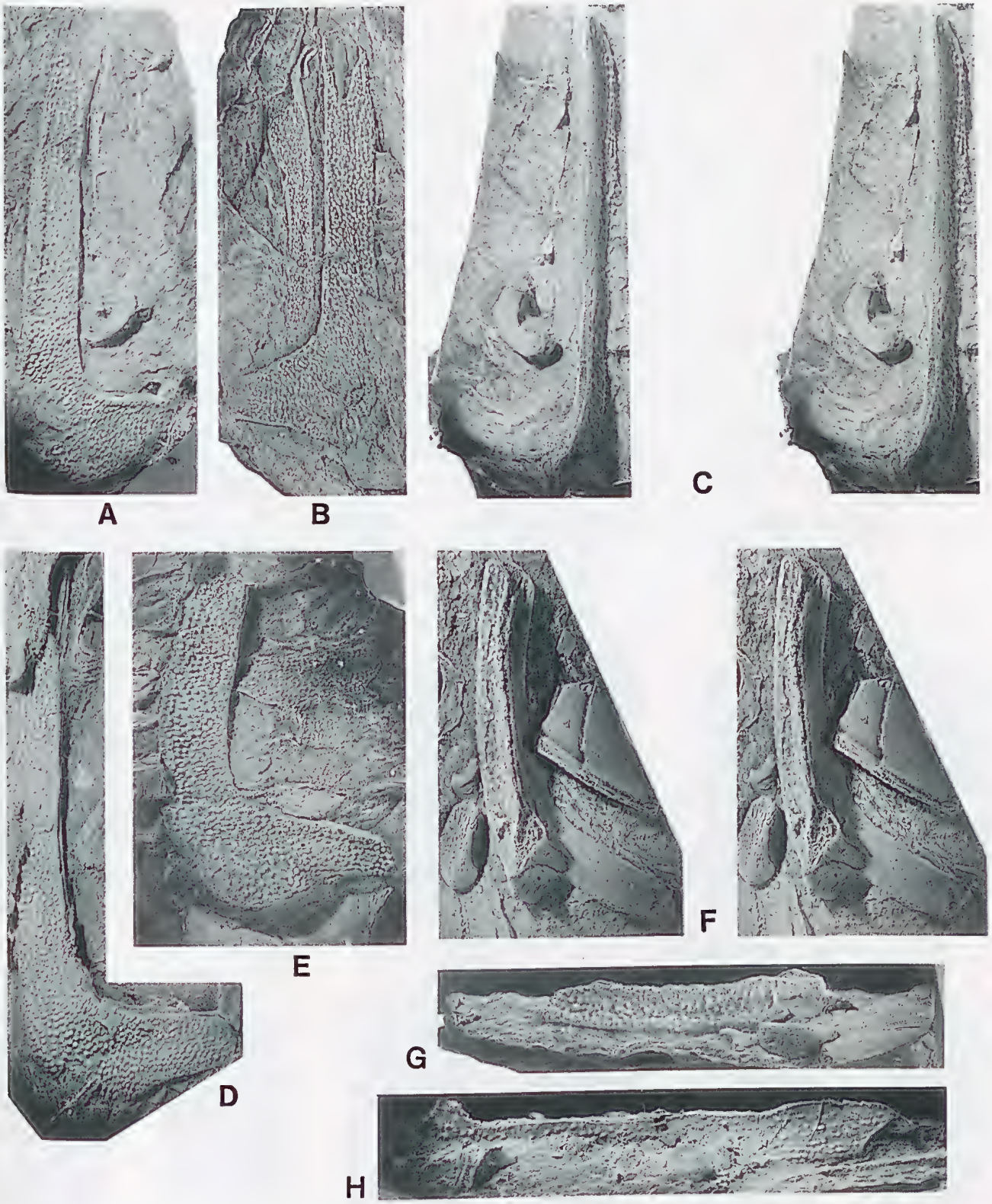

Fig.13. *Grenfellaspis branagani* n.gen.,n.sp. Late Devonian, NSW, Australia. Posterior ventrolateral (PVL) plates of trunk shield. Latex casts whitened with ammonium chloride. All specimens 1.5 times natural size. A - right posterior ventrolateral, AMF.56356, ventral (dermal) surface; B - left posterior ventrolateral, AMF.78695, ventral surface (NB also posterior lamina of associated ? left AVL); C - right posterior ventrolateral, AMF.56355 (counterpart of AMF.56356 (A), visceral surface (stereo pair); D - right posterior ventrolateral, AMF.56371, ventral surface; E - right posterior ventrolateral, CPC 29128, ventral surface; F-G - left posterior ventrolateral, AMF.56346, F - dorsal view (stereo pair), G - right lateral view; H - right posterior ventrolateral, AMF.56355, right lateral view of PVL seen in 'C' above.

consists of a long, narrow anterior division and a short, wide posterior division. AMF 56371 is a well preserved right PVL (62 mm long, 25 mm broad; L/B index 248). The anterior division of its ventral lamina is 49 mm long but only 7 mm wide. The posterior division, where the left PVL slightly overlaps the right, is narrowest at the midline (about 6.5 mm across). The lateral lamina of the PVL is very low, with a straight dorsal margin and of equal height throughout, except for a posterior dorsal corner (Fig.13G,H).

The anterior margin of the PVL plate is overlapped by the AVL, and the anterior division of the mesial margin, which in other antiarchs overlapped the median ventral plate, lacks an overlap area, as does the posterior division of the medial margin of the AVL just described. The overlap relationship with the PDL was similar to that between the AVL and ADL, with a dorsal groove which received the ventral edge of the PDL, with a developed overlap area only present in the posterior part of the margin (seen in AMF 56335). This type of overlap is suggestive of more primitive antiarchs (Yunnanolepiformes; also in *Remigolepis*; see Stensiö, 1931: 177,178).

Several specimens (AMF 56355, 56371, 56346) show the lateral and ventral laminae to be of equal length, and indicating that the subanal division of this plate which occurs in *Bothriolepis* is not developed in *Grenfellaspis*. Instead, the posterior margin of the trunk armour was concave (Fig.17), due to the lateral convexity on the posterior margin of the ventral lamina of each PVL (Fig.13D,E).

The visceral surface of the PVL plate shows the crista transversalis interna posterior strongly developed and very close to the posterior margin (Fig.13F). The contact surface of the PVL with the PDL is well preserved in AMF 56371, 56346 and 56355. The transverse crista runs vertically inside the lateral lamina and curves ventromesially to meet its antimere.

Last to be described are remains of the pectoral fin. No complete pectoral fin of *Grenfellaspis* has been located, and its structure is determined only from isolated plates.

Four types of pectoral appendage bones with terminal articulations have been identified (Fig.15), which are presumed to correspond to the four bones of the proximal segment of the fin in euantiarchs which carry articular processes. That identified as a Cd1 is represented by several examples (AMF 56274/148; 78693, 78778; CPC 29129, 29130). These vary somewhat in shape and proportions (Fig.14C,E), probably due to distortion, but three measured specimens are just over twice as long as broad. All show a prominent flattened articular process projecting at an angle to the long axis of the bone (ar3d, Fig.15A), and separated from it by a constricted neck. In two

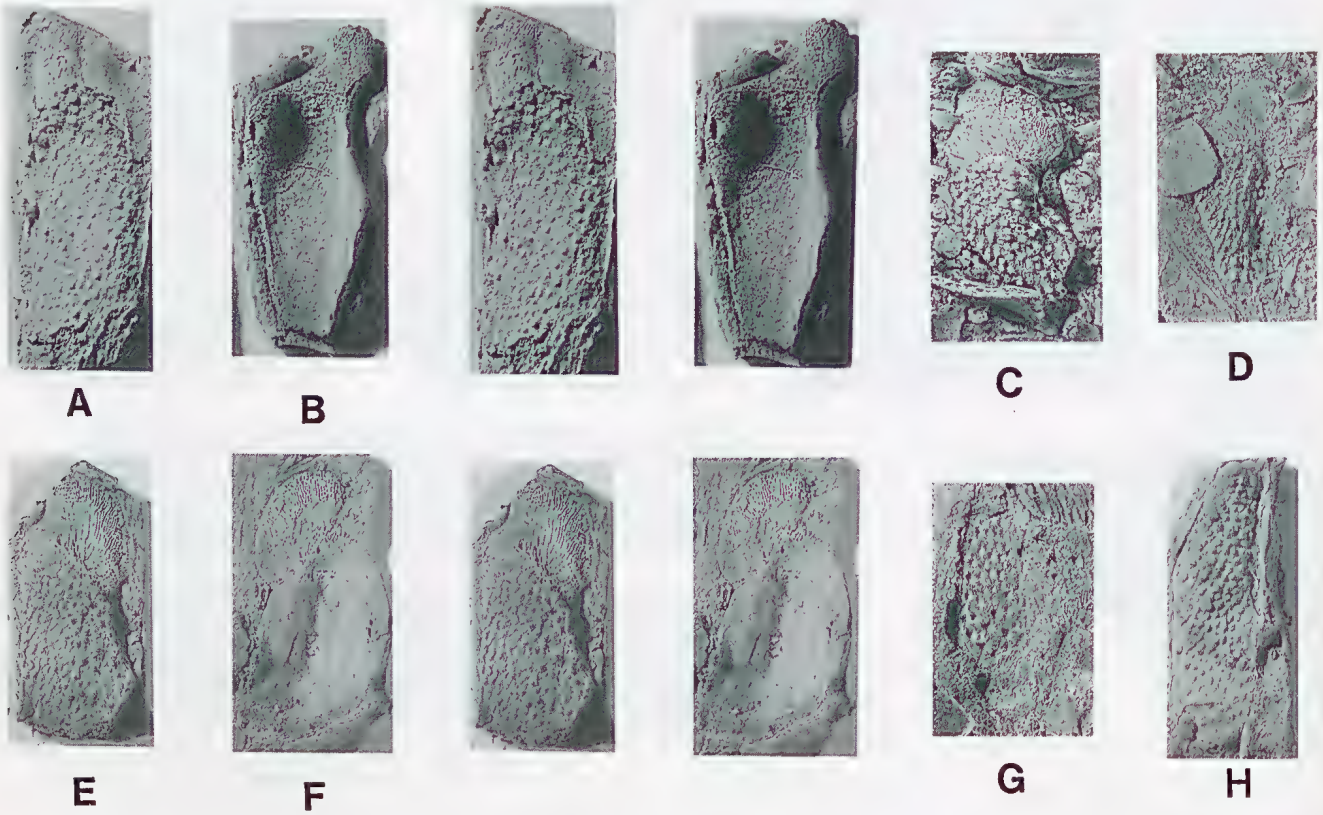

Fig.14. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Pectoral fin elements. Latex casts whitened with ammonium chloride. All specimens twice (x2) natural size. A-B - Cv1 plate, AMF.56280 (dermal) and 56281 (visceral) (stereo pairs); C - Cd1 plate, CPC 29129; D - Cv1 plate, AMF.79211; E-F - Cd1 plate, E - AMF.56148, dermal, F - AMF.56274, visceral (stereo pairs). G - ?Cd2 plate, AMF.79213; H - ?Cv2 plate, AMF.56148.

measured specimens the width of the process was 63-70% of total width. AMF 78693 (Fig.15A) in its short broad form is reminiscent of the Cd1 of *Remigolepis*, but its ornament of stellate tubercles is distinctive, and it differs from the Cd1 of *Remigolepis* or *Asterolepis* in the absence of a dorsomesial crest dividing the plate into dorsal and mesial laminae. A strong tubercular ridge at the mesial margin of the ornament in several specimens (r.dm) may be an equivalent feature. In asterolepids and bothriolepids generally the mesial lamina meets the main lamina of the bone at a right or acute angle, but in *Grenfellaspis* the ornamented part lies in a single plane (Fig.15B). All well preserved examples show three distinct margins for adjacent bones, which by comparison with other forms must be the Ml2 laterally, and Mm1 and Mm2 mesially. Thus, in contrast to *Asterolepis* (Gross, 1931, pl.5), the Mm1 must have formed part of the dorsal surface of the fin, a condition otherwise only reported in the Early Devonian *Procondylolepis* from China (Zhang, 1984). A distal angle indicates either point contact, or lack of contact, with the Cd2. One distorted specimen preserved in part and counterpart (AMF 56274) shows the inner surface of the articular process (Fig.14F). This carries an articular pad, but its surface is flat, in contrast to the strongly concave articular area of

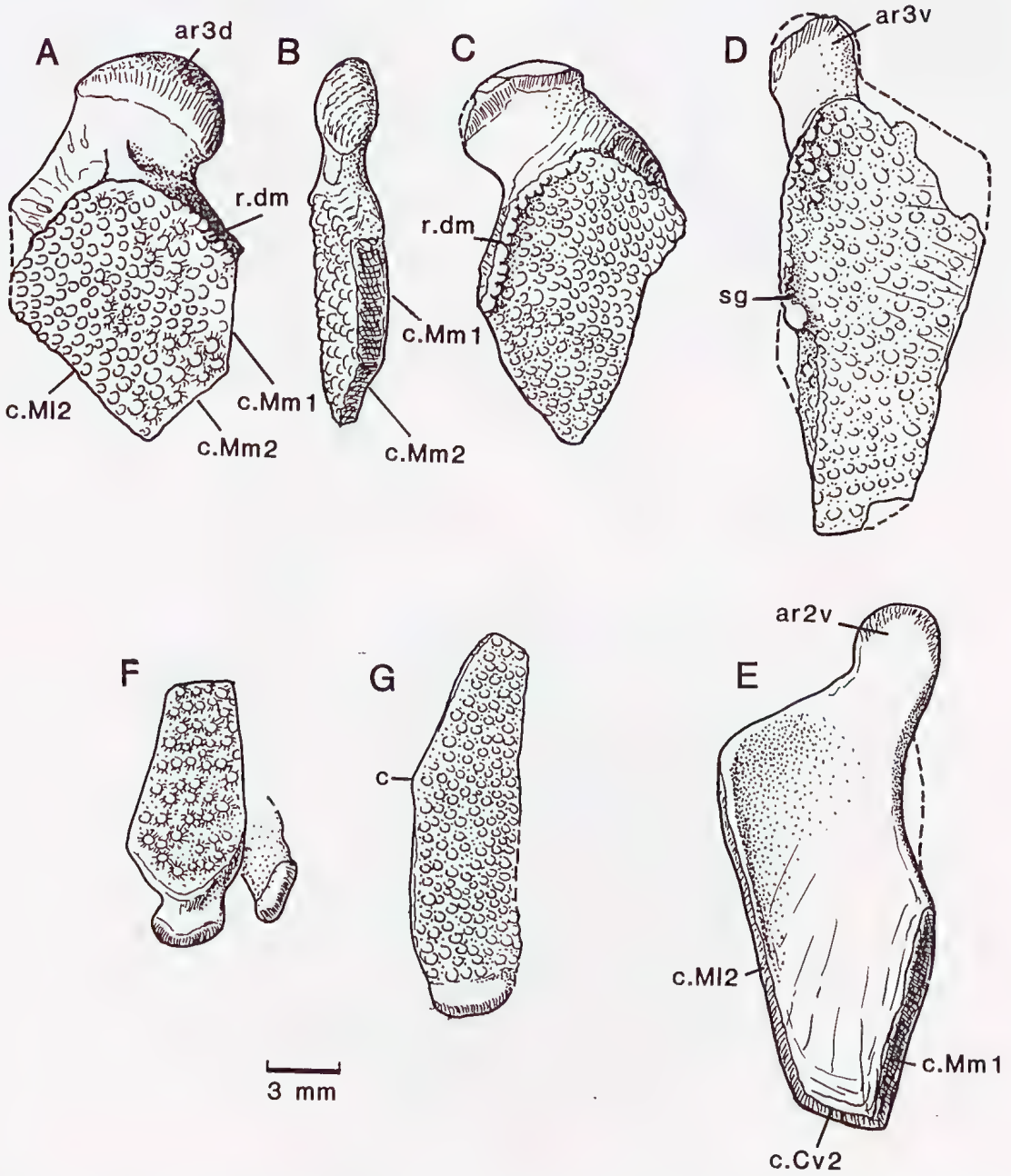

Fig.15. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Interpretation of pectoral fin elements in Figure 14. A-B - Cd1 plate, in external and side views, AMF.78693; C - Cd1?, CPC 29130; D - Cv1 plate, AMF.56280 dermal (Fig.14A); E - Cv1 plate, AMF.56281 visceral (Fig.14B); F - ?Cd2, AMF.79213 (Fig.14G); G - ?Cv2 plate, AMF.56148 (Fig.14H).

advanced antiarchs, in which both the Cd1 and Cv1 fit around the large hemispherical brachial process.

Two other specimens (AMF 56280,281; 79211) are interpreted as Cv1 plates. They have a much smaller narrow articular process than the Cd1, in the most complete specimen (Fig.14A,B,15D,E) only 19% of total width. Again the process projects strongly from the main part of the bone in what must be a mesial direction. A *siebknochen*-type surface is seen on dorsal and ventral surfaces, both of which are slightly convex (ar2v, ar3v, Fig.15D,E). The external impression is incomplete (Fig.15D), but shows an ornamented crest running down the mesial edge of the dorsal lamina, with a notch adjacent to a large tubercle which leads into a shallow groove, possibly sensory (sg). In *Asterolepis* a sensory groove crosses the Cv2, not the Cv1, but AMF 56280, with its two distinct and unequal laminae meeting at a high angle, has quite a different morphology to the Cv2 of *Asterolepis* (cf. Stensiö, 1931, fig.65).

The counterpart (Figs 14B,15E) shows the anteromesial margin to be a long concave margin to the mesial lamina of the plate, which did not contact other bones and thus must have formed a border to the proximal brachial aperture of the fin. This free margin is about half the length of the bone itself, and its large size, together with the fact that the bone narrows towards the end opposite the articulation, demonstrates that this was part of the proximal articulation. That the proximal brachial aperture of the fin was large can also be inferred from the structure of the brachial articulation on the AVL (see above). Other margins of the Cv1 show contact with three adjacent bones, which by direct comparison with *Asterolepis* (Gross, 1931, pl.5) must be the Mm1 mesially, the Cv2 distally, and the Ml2 laterally. In *Asterolepis* a sensory groove crosses the Mm1 to pass distally onto the ventral surface of the fin across the Cv2, but in *Grenfellaspis* the sensory groove apparently passed off the Mm1 onto the Cv1. The bone is nearly 1.2 times as long as broad. AMF 79211 is a right Cv1 incompletely preserved in external view (Fig.14D).

The third type of articular element (Figs 14G,15F) is represented by only one specimen (AMF 79213). This is an elongate bone (L/B index 217) with a small articular process, which differs from the Cv1 in that the process projects from the broader end in the direction of the long axis of the bone, in its more elongate

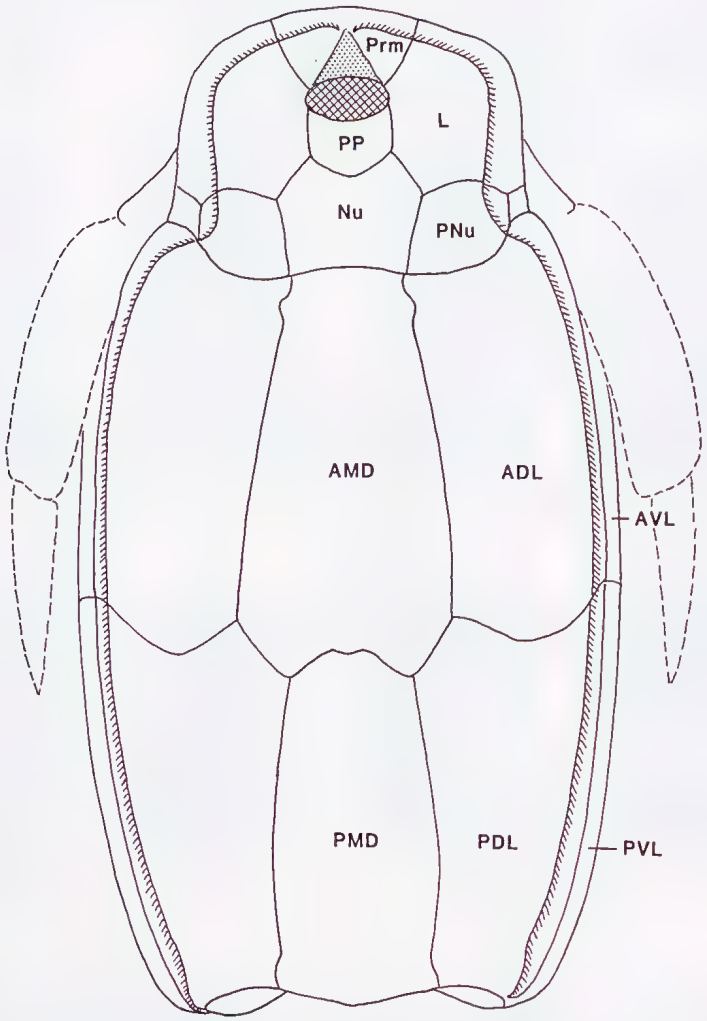

Fig.16. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Reconstruction of head and trunk shield in dorsal view. x1 actual size.

proportions, and in the relative size of the process (slightly smaller width than in the Cv1, but more than half the total breadth of the plate). The bone is flat with two long contact margins at each side and a short one at the opposite end to the articulation. By comparison with *Asterolepis* (Gross, 1931, pl.5) the longer free margin adjacent to the distal articular surface of the fin is mesial, and together with the marked corner near the articulation (c) suggests that this is a Cd2 from the right fin (*cf.* Stensiö, 1931, fig.64). An adjacent articular process exposed in visceral view may be the Cv2 from the same fin.

The fourth type of articular element (Figs 14H,15G) is again represented by a single example (AMF 56148). This is a more elongate bone (L/B index 280) with a small articular process of similar size to the previous specimen, but less distinct from the rest of the bone. One long margin is poorly preserved but appears fairly straight. The other has a slight angle about half way along (c), and there is a short terminal margin. This bone is assumed to be a Cv2 from the left side, by direct comparison with the corresponding plate of *Asterolepis* (Stensiö, 1931, fig.65).

In summary, the pectoral appendage of *Grenfellaspis* shows several special features compared to other euantiarchs: 1) distinct neck on the articular processes of the Cd1 and Cv1; 2) flat shape of their articular surfaces; 3) absence of a dorsomesial crest and mesial lamina on the Cd1, implying that Mm1 formed part of the dorsal surface of the fin; 4) much smaller articulation on the Cv1; 5) extension of sensory groove onto the Cv1 rather than the Cv2.

In these features *Grenfellaspis* shows a more primitive type of brachial articulation than in advanced antiarchs, in which the Cd1 and Cv1 of the pectoral appendage have large semicircular articular areas, of similar size and closely integrated to the ornamented part of the bone. In all known euantiarchs these features are always associated with a large hemispherical brachial process, and a mesial lamina on the Cd1.

On the other hand various features just described correspond to those seen in the pectoral appendage of *Asterolepis*, and presumably originated earlier in antiarch phylogeny: 6) Cv1 was longer than Cd1; 7) Cd2 was broader than Cv2; 8) there was a short or point contact between Cd1 and Cd2; 9) the articulations on Cd2 and Cv2 are of similar size.

The ornament of *Grenfellaspis* consists of crowded but randomly distributed tubercles often showing stellate bases. Only occasionally do the tubercles show slight linear alignment (Figs 6A,9E). A radial alignment is present in some examples of *Sinolepis* (see below). The ornament is often sparse in some regions (e.g., lateral to the sensory groove on the PNu, and L plates, and adjacent to the brachial articulation on the AVL), but this is variable amongst individuals.

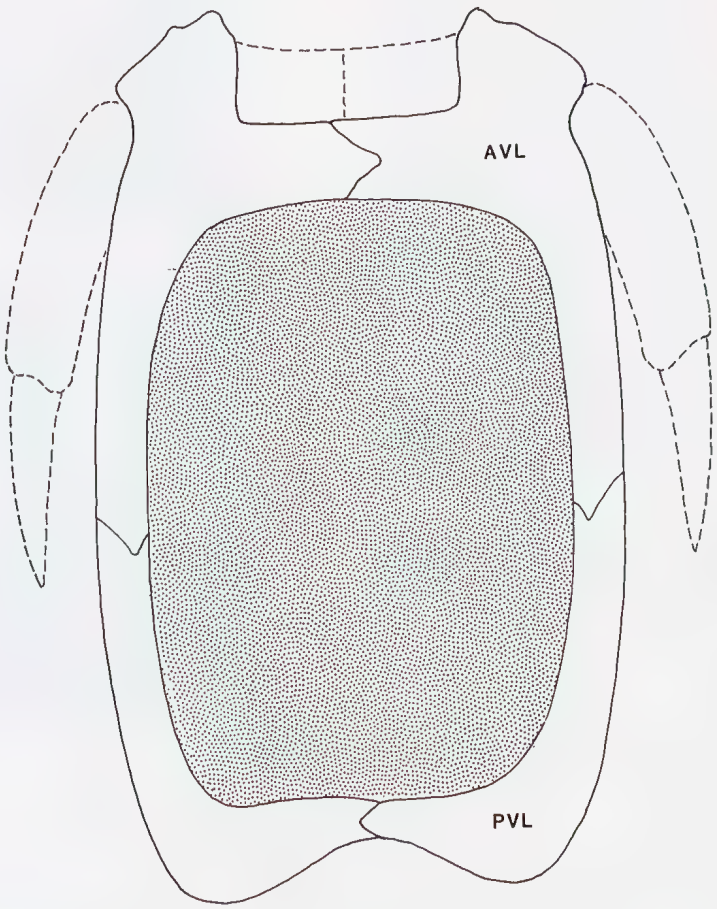

Fig.17. *Grenfellaspis branagani* n.gen., n.sp. Late Devonian, NSW, Australia. Reconstruction of ventral trunk shield. x1 actual size.

Dayaoshania Wang n.gen.

Etymology. From Dayaoshan Mountain of north-east Guangxi, China, the type locality.

Diagnosis. Middle sized Sinolepidae, with the skull broader than long (B/L index 140), and about or slightly over one third the length of the trunk armour. Rostral margin convex. Orbital fenestra small, and about one third the width of the skull. Trunk armour flat, with low lateral walls. AMD and PMD in the dorsal wall narrower than ADL and PDL. AMD with a B/L index of 50-60, the anterior margin narrower than the posterior, and the anterior division of the plate longer than the posterior. PMD plate smaller than AMD, with posterior and lateral corners developed. Levator fossa, postlevator thickening, and median ventral grooves apparently not developed, but anterior and posterior pits present on the ventral aspect of the shield. Semilunar plates small. Pectoral appendage robust, and almost as long as the ventral wall of the trunk armour, with a distal segment almost as long as the proximal. Arrangement of pectoral appendage bones of pterichthyodid type, with long Cd1 and Ml2, and large Mm1 comprising dorsal and mesial laminae. Spines on the inner margin of the proximal segment. Main lateral line sensory groove passes dorsally to dorsolateral ridge of trunk armour.

Remarks. Some of the features included here (such as overall size) may be specific rather than generic characters. The latter are discussed below in the section on sinolepid inter-relationships. *Dayaoshania* shares many features with *Grenfellaspis* described above, but differs in the proportions of the AMD and PMD plates (wider in *Grenfellaspis*), and the strongly developed anterior and posterior ventral pits and processes. *Dayaoshania* differs from *Sinolepis* (Liu & P'an, 1958) in the much smaller size of the head shield relative to the trunk armour, the ornament, and the distinct overlap of the L onto the PP and Nu plates. Various other characters of *Dayaoshania* are no doubt primitive features for sinolepids or antiarchs generally. These may include the absence of a median ventral ridge and groove on the trunk armour, the small orbital fenestra situated close to the rostral margin, and the large size of the Mm1 in the dorsal surface of the pectoral appendage.

The basis for distinguishing *Dayaoshania* from *Xichonolepis* is discussed below in the 'Remarks' section for the latter genus.

Dayaoshania youngi Wang n.sp.

Figs 18-22

Type material. HOLOTYPE, MGV 1947, 1948, an almost complete external mould of the headshield and dorsal trunk armour, with the dorsal trunk shield preserved in the counterpart (MGV 1948).

Other material. An articulated individual with pectoral appendages preserved in part and counterpart (MGV 1950,51), and incomplete remains of the dorsal shield (IVF 2,4,5).

Locality and horizon. Yuantou, Pingle County, Guangxi Province, from a single horizon in the upper part of the Dayaoshan Group, of Lower or Middle Devonian age (?Emsian-Eifelian). Associated fossils include abundant polybranchiaspids (a new genus and species) and rare arthrodires.

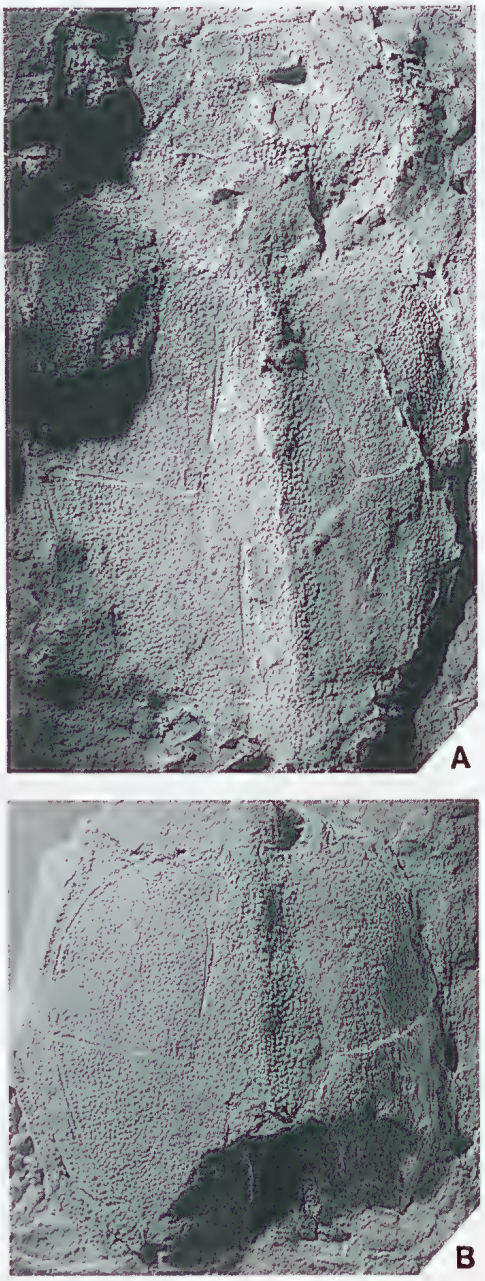

Fig.18. *Dayaoshania youngi* n.gen., n.sp. Dayaoshan Mountain, Pingle County, Guangxi Province, China. Dayaoshan Group, Early or Middle Devonian (?Emsian-Eifelian). A - holotype, dorsal impression of head and trunk shield, MGV.1947. Latex cast, whitened with ammonium chloride. x1.7 natural size. B - holotype, dorsal surface, trunk shield, V.1948. Original specimen, whitened with ammonium chloride. x1.3 natural size.

Etymology. In honour of the late eminent Chinese vertebrate palaeontologist Professor Young Chung-chien.

Diagnosis. As for genus (only species).

Description. The five known specimens of *Dayaoshania youngi* n.gen., n.sp. are all of similar size (Table 3), and were closely associated on one horizon. We assume, for the present, that the species did not attain a large size. The holotype (Fig.18A) shows the head and trunk shields preserved in association, but slightly dislodged. The combined head and trunk length as preserved is 71 mm, with an estimated original length of about 68 mm. MGV 1950 (Fig.19) is 56 mm in total length, and 48 mm wide, with the AMD and some plates of the pectoral appendage displaced.

The **head shield** is reasonably preserved as an external mould in the holotype. It is flat, and slightly hexagonal in shape, with a convex rostral margin (22 mm long) and lateral margin 12 mm long. Obstantic and posterior margins are not preserved, but the length of the posterior margin is estimated at about 20 mm. Total length of the head shield is 20 mm, and its greatest width (between lateral corners) is 28 mm. The margins of the PrM and L plates are distinct. The anterior margin of the PNu and anterolateral margin of Nu are seen on both sides, but the posterior part of the Nu is not preserved. The anterior margin of the PP apparently forms only the middle part of the posterior margin of the orbital fenestra, in contrast to *Grenfellaspis* or *Sinolepis* where it forms most or all of this margin. However the anterolateral margins of the PP are unclear, and its posterior margin is not preserved.

The orbital fenestra is small and elliptical in shape, and more than twice as broad as long (B/L index 180). It is anteriorly placed (7.2 mm from the rostral, and about 9 mm from the posterior margin).

The PrM plate is 13.3 mm wide at its anterior margin, and 7.6 mm long (B/L index 57). The orbital margin is 7.4 mm across. The infraorbital canals do not meet in the midline, as is normal in antiarchs. The preorbital depression is preserved in MGV 1947, and appears triangular in shape with rounded corners.

The L plate is a large polygonal bone, 13 mm long and 8.2 mm wide (B/L index 63). As in other antiarchs the ifc crosses this plate from the PrM to the PNu. On the right side of the holotype a prelateral notch is seen, but on the left the lateral margin is obscured by the SM plate (Fig.18A). The lateral corners on the PP (Fig.21) are not comparable to those on the PP of *Sinolepis*, which are formed by the unique overlap of this bone onto the L in that form.

The Nu plate was apparently large and hexagonal in shape (Fig.21), but only the anterior division of one lateral margin is clearly seen. The PNu is smaller and squarish in shape, and is crossed by the ifc.

The submarginal (SM) plate of the cheek, preserved on the left side of the holotype (Fig.18A), is 11 mm long and 4.5 mm wide, and of elongate elliptical shape. There is no evidence of a separate prelateral (PrL) plate. The postmarginal (PM) plate is not well preserved, but its mesial borders are seen on the right side of the holotype.

The ventral aspect of the head shield is partly preserved in MGV 1950, but only the rostral margin is clear (Fig.19). The posterior part is obscured by the impression of the semilunar plates, and on the counterpart by the subcephalic division of the AVL plates (Fig.20).

There are five examples showing the structure of the **trunk shield** in dorsal view, of which the holotype (Fig.18) shows the complete dorsal wall. The PMD is incomplete in IVF 4, but in this specimen the overlap relations of the AMD are well shown. The AMD and PDL are also preserved on MGV 1950, and most of the PMD is seen on MGV 1951. These specimens show the dorsal wall of the trunk armour to have been rather flat, but with a convex median dorsal ridge. The lateral wall is low. In the holotype the dorsal wall is 53 mm long and 45 mm wide.

The AMD is longer than wide (Table 3), with well-developed lateral corners situated about three quarters of the length from the narrow, straight anterior margin. The external posterior margin is wider than the anterior. The internal posterior margin shown on MGV 1950 (Fig.19B) appears to be convex, whereas in *Xichonolepis* it is transverse. The ratio of external length of AMD to PMD (106-117) is comparable to *Xichonolepis*, but in *Dayaoshania* this is affected by the much stronger posterior process on the PMD. Taking this into account the PMD in *Dayaoshania* is proportionally smaller compared to the AMD.

The ventral structures of the dorsal wall can only be seen in MGV1950, which shows the impression of the anterior ventral pit and process on the displaced AMD (pt1, Fig.19B). The anterolateral thickening appears weak or absent, and a weak median ventral groove is developed posteriorly, as in small *Xichonolepis*.

The PMD is well preserved in the dorsal impression of the holotype (Fig.18A). It is similar in shape to *Xichonolepis*, but with a stronger posterior process. The posterior ventral pit and process are not preserved on any specimen, but presumably were developed as in other sinolepids. Proportions are given in Table 4.

The overlap relationships between the AMD and PMD are not clearly preserved on the holotype, but are more distinct on V.1950, IVF 2 and IVF 4, where the anterior margin of the PMD overlaps the posterior margin of the AMD.

The ADL is broad (B/L index 60). The dorsal lamina in the holotype is 23 mm long and 18 mm wide, but the lateral lamina is very low (only about 2 mm high), and difficult to measure with any accuracy. In the holotype the left obstantic process of the ADL is broken. No other specimen shows the anterior inner transverse ridge or obstantic process. The main lateral line canal passes across the plate, and in MGV 1948 (Fig.18A) and other specimens is clearly seen to lie dorsomesial to the lateral margin of the plate, on its dorsal lamina, and there is no clear dorsolateral ridge or lateral lamina. In contrast, in bothriolepids the lateral line sensory groove

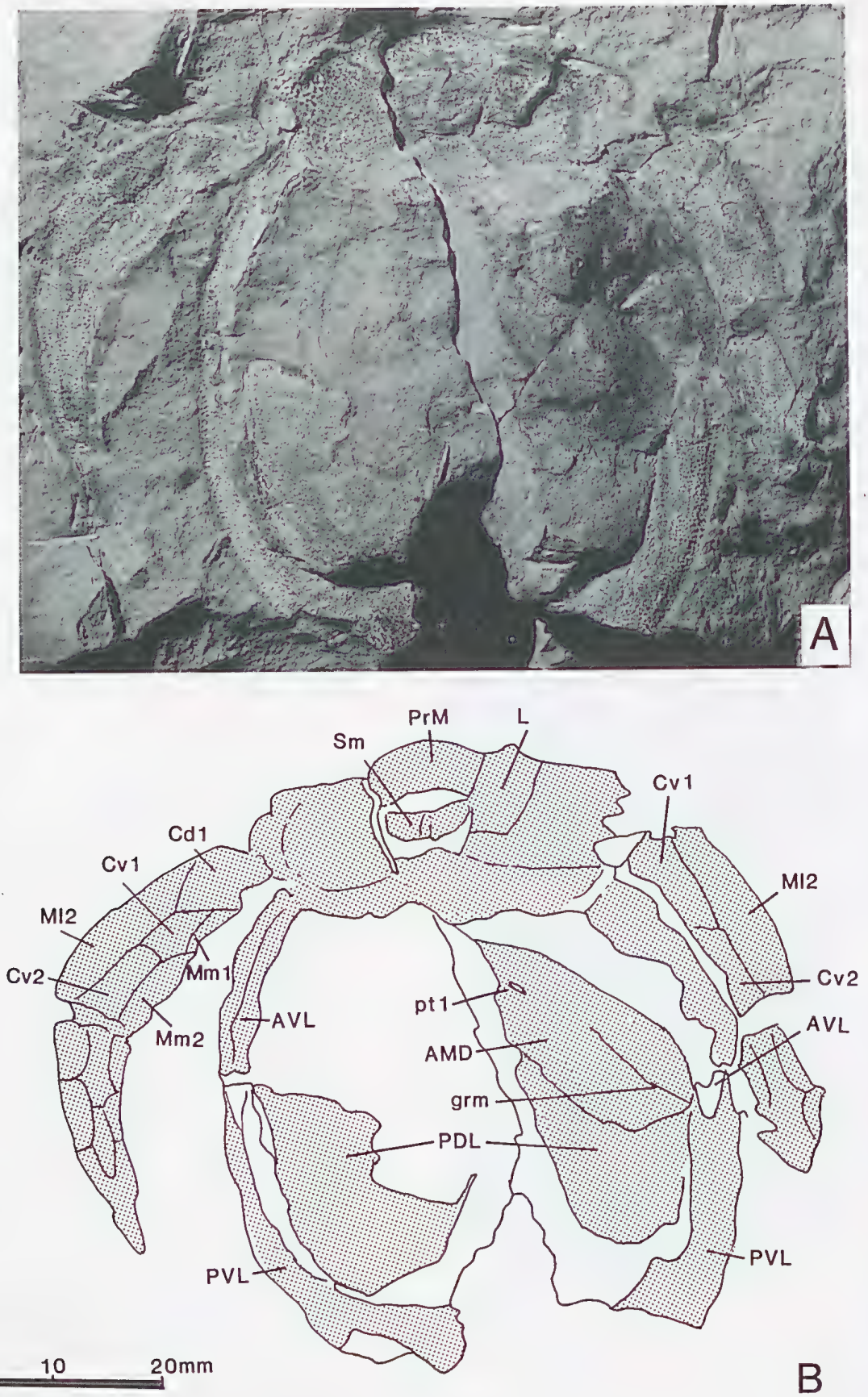

Fig.19. *Dayaoshania youngi* n.gen., n.sp. Dayaoshan Mountain, Pingle County, Guangxi Province, China. Dayaoshan Group, Early or Middle Devonian (?Emsian-Eifelian). A - almost complete specimen, MGV.1950, in dorsal view. B - interpretation of MGV.1950.

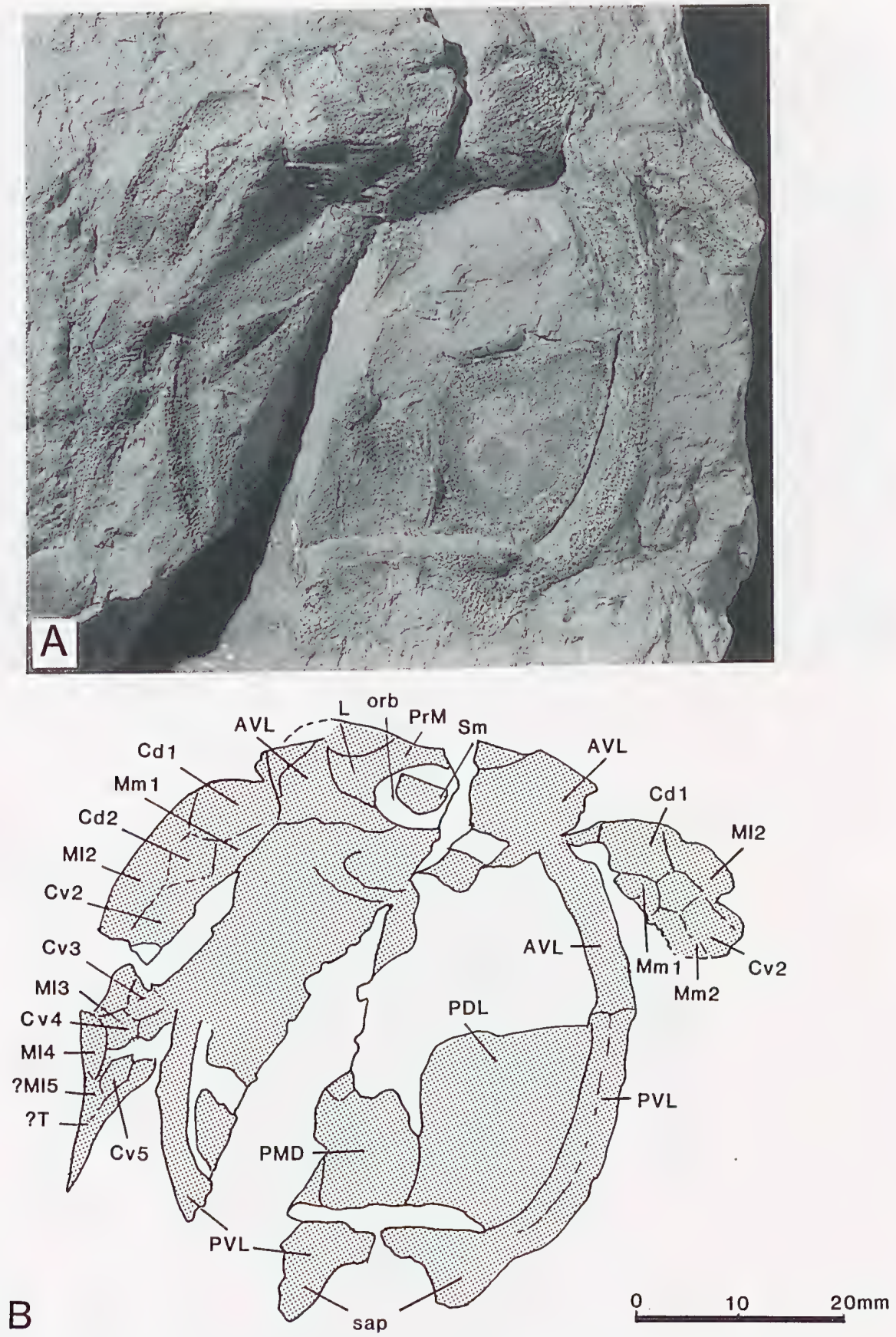

Fig.20. *Dayaoshania youngi* n.gen., n.sp. Dayaoshan Mountain, Pingle County, Guangxi Province, China. Dayaoshan Group, Early or Middle Devonian (?Emsian-Eifelian). A - almost complete specimen, MGV.1951 (counterpart of MGV.1950, Fig.19), seen in ventral view. B - interpretation of MGV.1951.

crosses the lateral lamina of the ADL. The dorsal margin of the ADL is overlapped by the anterolateral margin of the AMD, as is normal, but the overlap area is very narrow, particularly the posterior part. Posteroventrally on the left side of MGV 1948 is a short margin in contact with the PVL, as in *Xichonolepis*.

The PDL has a large and broad dorsal lamina, 22 mm long in the holotype, with greatest breadth (18 mm) through the dorsal corner (B/L index 82). On the left side of MGV 1948 (Fig.18A) the suture with the PVL plate is clearly seen immediately lateral to the groove for the lateral line canal. Thus the PDL lacked a distinct dlr and lateral lamina, as is also the case in smaller individuals of *Xichonolepis* (see below). Whether the PDL and PL plates are fused to form a MxL plate is not clear from the available specimens. The overlap relations with surrounding bones is the same as in *Xichonolepis*. The area overlapped by the ADL is very narrow, and that overlapped by the PMD is narrow, and similar to *Xichonolepis* and *Grenfellaspis*. The lateral line sensory groove is much closer to the lateral margin than on the ADL (Figs 18B,21).

On the second articulated specimen (MGV 1950, 51) the skull bones are largely obscured by the AVL plates and are difficult to interpret, but the specimen is important in showing the ventral wall of the trunk armour and the pectoral appendage. MGV 1950 (Fig.19) exhibits the internal mould of dorsal trunk shield bones (AMD, PDL), the anterior and posterior parts of the ventral wall preserved as incomplete external moulds of the AVL and PVL plates, and a part impression of the almost complete left pectoral appendage. The exposed skull bones in this specimen (PrM, L, Fig.19B) are problematic in that their surfaces show impressions of the ornament, as on the adjacent AVL plates, and we must presume therefore that the skull was turned over before preservation. In MGV 1951 the preservation is reversed, and this specimen shows most clearly the subcephalic and subanal divisions of the ventral wall, and the distal segment of the right fin (Fig.20). Both specimens were flattened during burial. On the available evidence there was no MV plate in *Dayaoshania*, as was suggested above for *Grenfellaspis*, and inferred also for *Xichonolepis* and *Sinolepis* (see below). The ventral wall consists only of the narrow and elongate ventral laminae of the ventrolateral plates, with apparently no dermal armour over the central part. In external view the ventral laminae of both AVL and PVL are 4 mm wide; the former is 30 mm long, and the PVL slightly longer (34 mm). The AVL overlaps the PVL, and the shape of the overlap is most clearly seen on the left side of MGV 1950 (Fig.19B). The subcephalic division of the AVL is distinct in both specimens, but the overlap relationship between right and left plates at their median suture could not be determined. The paired semilunar plates are preserved in both specimens compressed against the orbital fenestra (Sm, Figs 19B, 20B). Their small size, and the smaller semilunar notch, are clearly different

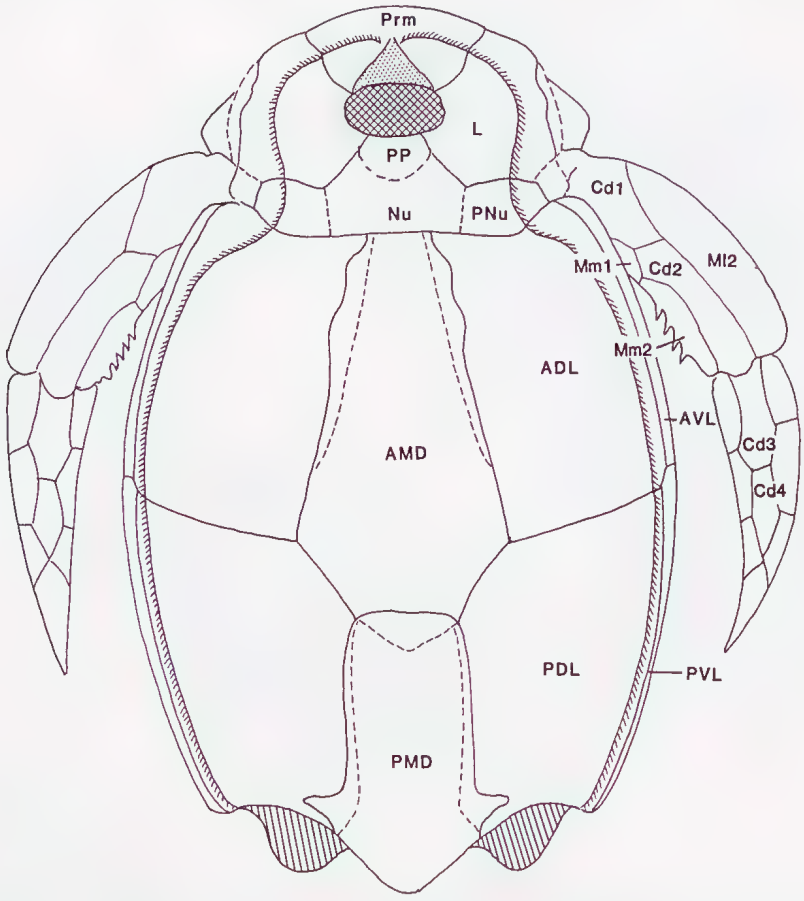

Fig.21. *Dayaoshania youngi* n.gen., n.sp. Devonian, China. Reconstruction of dorsal surface x1.8.

from the condition in *Grenfellaspis* or *Xichonolepis* (Figs 17,31). The PVL in MGV 1951 is 4 mm wide and 34 mm long. The posterior part of the PVL is wide, with the left plate meeting and overlapping the right in the midline. The posterior margin is strongly concave with prominent, rounded lateral subanal processes (sap, Fig.20B). A similar shape is seen in *Grenfellaspis* and *Xichonolepis* (Figs 17,31), but in *Dayaoshania* the lateral processes are much stronger. There is no true subanal division with extensive midline suture as is seen in bothriolepid and asterolepid antiarchs. *Dayaoshania* and other sinolepids may be primitive in this respect since yunnanolepids also lack a true subanal division.

In MGV 1950 the left pectoral appendage is preserved mainly as an impression of the ventral surface, with part of the dorsal surface preserved as bone (Fig.19). The right appendage shows part of the external impression of the ventral surface, and part of the internal surface of the dorsal wall, but the distal segment is incomplete. For the complete left fin, the proximal segment is 21 mm long and 9.1 mm wide, and the distal segment is 22 mm long and 6 mm wide at its proximal end. The left proximal segment displays the Cd1, which is apparently a short plate, as shown by the suture on the counterpart (MGV 1951), in which the bone is preserved (right side of Fig.20). The Ml2 on this specimen is preserved as an external impression of the dorsal ornament. The mesial side of the fin is occupied by two bones separated by a clear suture, which must be the Mm1 and Mm2 plates (Fig.20B). Although not very clear, it seems that their dorsal surfaces are preserved as impressions, with the spinose margin therefore representing the dorsomesial ridge of the fin (cr.dm). At the incomplete distal end of this fin the bone adjacent to the Mm2 shows ornament, and must be the Cv2. Its mesial edge presumably approximates to the mesial margin of the ventral surface of the fin (displaced laterally), as in *Bothriolepis* (e.g., Stensiö, 1948, fig.195). The suture between the Mm1 and Mm2 divides laterally to give the appearance of an additional small bone, but the proximal side of this suture is with the Cd1, and the distal side sutures with the Cv2, indicating that dorsal and ventral surfaces of the fin have been compressed together. Thus this specimen shows that the Cv1 was longer than the Cd1, as in other antiarchs. The Cd1 on this specimen is preserved mainly as an impression of the ornamented surface. An articular head of the fin is present as poorly preserved bone (right side of Fig.20B). This projects mesially, and its relatively small size compared to most other antiarchs recalls the Cv1 of *Grenfellaspis* described above. A trace of bone connecting this articular process to the AVL is probably a remnant of the brachial process.The opposite side of MGV 1951 again preserves the inner bone surface of the dorsal side at its proximal end, which confirms that the Cd1 was short. The inside of the Ml2 is clear, and

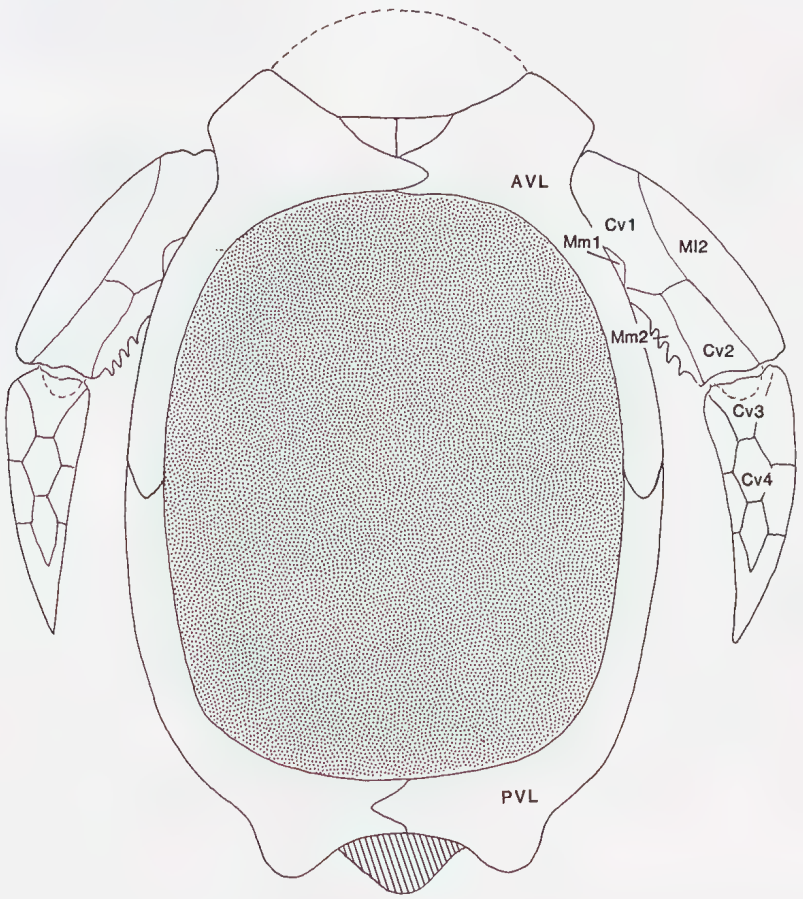

Fig.22. *Dayaoshania youngi* n.gen., n.sp. Devonian, China. Reconstruction of ventral surface. x1.8.

the Mm1 again shows the same suture on its dorsal lamina, partly obscured by the ventral lamina. However the distal part of the dorsal wall is covered by the well preserved ventral bone surface. On the basis of the similar suture pattern displayed on both sides of MGV 1951, we interpret the Cd2 of *Dayaoshania* to have been longer than the Cd1, and of unusual shape with an expanded proximal end (Fig.21). The distal end and articular surface of the Cd2 are not preserved.

The distal part of the ventral wall of the proximal segment is well preserved as bone showing the ornamented surface on the more complete (right) fin of MGV 1951 (Fig.20). A clear suture down the middle of the fin separates two bones. The lateral one must be the ventral lamina of the Ml2, and the mesial one is the Cv2, with no indication of the Mm2 on this specimen. The counterpart of this fin on MGV 1950 (right side of Fig.19B) shows the proximal end of the Cv2 and the suture between the Ml2 and Cv1, but the proximal end of the Cv1 is missing. The impression of the left fin of this specimen shows the Cv2 with its distal articulation, and a narrow strip of the Mm2 exposed along the mesial edge of the fin.

In MGV 1950 the impression of the ventral aspect of the distal segment is preserved for the left fin, but sutures between bones are unclear. The distal segment for the right fin in MGV 1951 shows the bones slightly displaced, with apparently three bones in the ventral central and lateral marginal series (Fig.20B).

The ornament of *Dayaoshania* comprises fine stellate tubercles evenly distributed over the external surface of the bones, with coarser ornament on the median dorsal ridge of the trunk armour. The sensory canal system shows no special features except that the main lateral line groove on the trunk runs back across the dorsal wall because the dorsolateral ridge is absent.

Xichonolepis P'an & Wang, 1978

Emended diagnosis. Sinolepid of large size. Head shield much shorter than trunk armour; postpineal and nuchal plates do not overlap lateral plate. Trunk armour broad, dorsal wall flat, lateral wall convex; dorsal median and dorsolateral ridges generally not developed. Semilunar plate(s) large. AMD large, six-sided, lateral corners well developed, wider than ADL or PDL; anterior margin of AMD slightly narrower than posterior margin. Postnuchal notch and external postlevator process of anterolateral margin of AMD developed. PMD narrower than AMD; lateral process long, extending beyond lateral margins. Posterior marginal area wide and long, with straight anterior margin, posterior ventral pit and posterior ventral process on posterior marginal area.

Remarks. Some characters, such as large size, are probably specific features, but until more than one species is described no attempt is made to separate them. The characters used here are discussed generally in the section on sinolepid inter-relationships.

Xichonolepis resembles *Dayaoshania* in the shape of the PrM, AMD and PMD bones, and in the general morphology and proportions of the trunk armour. However, *Dayaoshania* differs as follows (Table 6): 1) the slight anterior median ventral groove and ridge; 2) the more elongate AMD in *Dayaoshania* (B/L index 50-60, compared to 60-80 for *Xichonolepis*); 3) the small semilunar plates; 4) the convex internal posterior margin of the AMD; 5) the stronger posterior process on PMD, which is proportionately shorter compared to the AMD; 6) the broader PDL; 7) the stronger lateral subanal process on the PVL; 8) a different shape in the overlap between the AVL and PVL plates; 9) a presumably smaller adult size of *Dayaoshania*.

Xichonolepis qujingensis P'an & Wang

Figs 23-31

Xichonolepis qujingensis P'an & Wang, 1978: 334, pl.33, figs 1-6.
Xichonolepis qujingensis.–Zhang, 1980: 272-280, pls 1-3.

Type material. HOLOTYPE, an incomplete PMD (MGV 1546) collected from Xichong, near Qujing, and first described by P'an & Wang (1978: 324-325, pl.33, figs 1,2) as an AMD (see Zhang, 1980, pl.2, fig.3).

Other material. Original material collected from Xichong by P'an & Wang (1978), and subsequently by Wang (three PrM plates, MGV 1547, IVF 501, 502; one PNu, MGV 1549; a possible L, MGV 1548, an Ml2 from the pectoral fin , MGV 1550); one specimen collected from Dashishan near Kunming (AMD, V 4440.1a); an AMD (V 9058) and PDL (V 4442.14a) from Panxi, Huaning (collected by IVPP members; Zhang, 1980); an AMD (V 5077) from Zhangjiaying, Qujing; material collected from Zhaojiazhuang and the nearby cement quarry near Wuding by IVPP members and Zhang and colleagues (AMD, V 2965.9, 9057.8; PMD, V 2965.1,2, V 5076.2a; ADL, V 9056.1, 9057.4; PDL, V 2965.4, 9057.1.2; AVL, V 9057.7a,b; PVL, V 9056.2, 9057.3; complete dorsal wall of trunk armour, V 5076.1a,b; subcephalic division of ventral wall of trunk armour, V 5076.6; incomplete ventral wall of trunk armour, V 2965.7; distal segment of pectoral fin, V 2965.7).

Localities and horizon. From the following localities in Yunnan Province: Xichong and Zhangjiaying, near Qujing; Dashishan, near Tonghai; Panxi, near Huaning; Zhaojiazhuang and the nearby cement quarry near Wuding (Fig.2). All in sandstones or dolomitic limestones beneath the Haikou Formation (Middle Devonian), and equivalent to the Sanshuanghe and Chuandong Formations of Yang *et al.* (1981, table 4). At Zhaojiazhuang the same fish fauna (including *Dianolepis* and *Bothriolepis tungseni*) occurs in the limestone and underlying sandstones. The fish horizon is considered to be older than the typical Haikou Formation in the vicinity of Kunming, which is Givetian in age.

Diagnosis. As for genus (only species).

Remarks. *Xichonolepis qujingensis* was established by P'an & Wang (1978) and later amended and amplified by Zhang (1980). The material then available for study consisted of a few individual plates of the skull and dorsal wall of the trunk armour, but the morphological characters of the ventral and lateral walls of the trunk armour remained largely unknown. On this evidence *Xichonolepis* was tentatively allocated to two different antiarch families, the Bothriolepidae and Asterolepidae.

New material collected in recent years from the original localities and horizons of Yunnan include examples of the ventral wall of the trunk armour and AVL and PVL plates. They show clearly that *Xichonolepis* belongs neither to the Bothriolepidae nor to the Asterolepidae, but is closely related to the genera *Grenfellaspis* n.gen. and *Dayaoshania* n.gen., described above, and to *Sinolepis* (Liu & P'an, 1958).

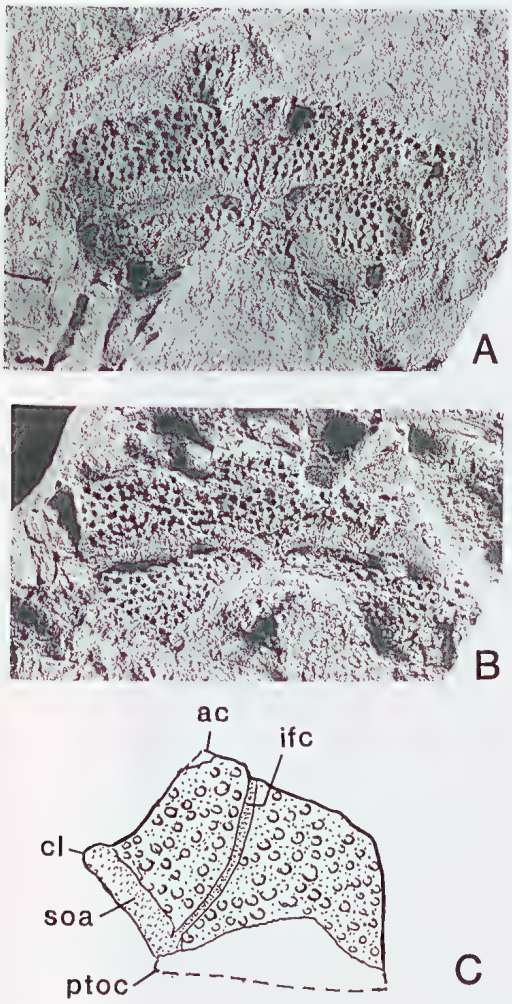

Fig.23. *Xichonolepis qujingensis* P'an & Wang; Xichong, near Qujing County, Yunnan Province, South China. Sandstones or limestones beneath Haikou Formation, Middle Devonian (Givetian). A,B - 2 premedian plates (IVF 501,502), preserved as natural moulds. Both x2.4. C - outline of right PNu, based on reinterpretation of specimen MGV.1549 from Qujing County; figured by P'an & Wang (1978, pl.33, fig.5).

Description. The headshield of *Xichonolepis qujingensis* is represented only by isolated bones. MGV 1547 (originally figured as a Nu plate) is an inverted PrM, and MGV 1549, described by P'an & Wang (1978) as a L plate, is regarded as an inverted PNu (Fig.23C). The PrM is known from three external impressions (Fig.23A,B; P'an & Wang, 1978, fig.13). Two are almost complete (MGV 1547, IVF 501), and show that the plate is broader than long (B/L indices 206 and 210 respectively), and somewhat broader than in *Dayaoshania*. The anterior margin is much broader than the posterior, and in IVF 501 is convex (Fig.23A). The straight margin on the previously figured specimen (P'an & Wang, 1978, pl.33, fig.3) is probably incomplete. The lateral margin is convex. On the whole the plate is very similar in shape to that of *Sinolepis*, except that the anterior division of the plate in *Sinolepis* is very short, with the infraorbital groove much closer to the rostral margin. All three specimens exhibit clearly the triangular preorbital depression. The infraorbital canal passes onto the plate from the middle of the lateral margin. Behind it is a deep groove which shows that the sensory ridge was strongly developed, as in *Grenfellaspis* described above. The ornament is evenly distributed on both sides of the sensory groove.

MGV 1549 was originally described as an incomplete L plate by P'an & Wang (1978, pl.33, fig.5), but we now consider the specimen to be an inverted dermal impression of a right PNu (Fig.23C). The posterior margin is missing, but the position of the sensory groove indicates that the posterolateral corner is nearly complete. In its pentagonal shape the plate is generally similar to the PNu of bothriolepids (Stensiö, 1948, fig.27). The lateral division is broad, in contrast to *Grenfellaspis* and *Sinolepis* (and asterolepids) in which it is very narrow. A conspicuous anterior corner (ac) is developed on the anterior margin between lateral and mesial divisions. The lateral margin, which contacted the PM plate, has an oblique anterolateral orientation, and is about the same length as the obstantic margin. The obstantic margin and subobstantic area (soa) are long, and the anterolateral corner (cl) is therefore situated much further anteriorly than in asterolepid antiarchs. This indicates that the obstantic process of the trunk armour was well developed, and that the PM plate of *Xichonolepis qujingensis* was of bothriolepid type, and similar to *Grenfellaspis* and *Dayaoshania* as described above. The infraorbital sensory groove is very clear. As preserved this plate resembles the PNu of *Dayaoshania* in being short and broad, whereas in *Grenfellaspis* and *Sinolepis* (see below) the PNu is more elongate.

The incomplete external impression of the L plate (MGV 1548) figured by P'an & Wang (1978, pl.33, fig.4) is apparently a left plate showing a broad lateral division. It is similar to that of *Dayaoshania*, and differs from *Grenfellaspis* and *Sinolepis* in which the lateral

division is very narrow. Based on the previously published figure the ridge adjacent to the sensory groove may also be present.

New information on the trunk armour of *Xichonolepis* comes from additional specimens of separate bones collected from the Haikou Formation at Wuding (preserved in limestone and mostly exposed in internal view), and preparation of latex casts of internal and external impressions of the trunk armour in previously described specimens (V5076.1, 6), collected from the underlying sandstone unit (which contains the same fish fauna). A latex cast of V 5076.1b (Fig.24) shows the broad and flat dorsal wall of the trunk armour, which is only slightly elevated, and lacks both a median dorsal ridge and sensory groove. The lateral wall is very low (Fig.25B). This specimen lacks the anterior margin of the trunk armour, and the processus obstans of the ADL plate is missing (Fig.25A). Preserved trunk armour length is 210 mm and breadth 174 mm (B/L index 83). The right lateral wall is relatively complete, 184 mm long and 13 mm high, and thus 13.5 times as long as high. The laminae meet at an obtuse angle. The main sensory canal runs back just beneath the dlr. The AMD is large and broad with well-developed lateral corners. The narrow anterior and broad posterior margins are well shown in other specimens (Fig.26A,B). In shape the plate is strikingly different from the AMD of *Sinolepis* or *Grenfellaspis*, and is the broadest bone in the dorsal wall. The anterior division is three times the length of the posterior division, and the posterolateral margin is short. The PMD of V 5076.1 (Figs 24,25) is narrow and slightly shorter than the AMD. The dorsal lamina of the ADL is quadrilateral, with the anterior end slightly broader than the posterior. Its lateral lamina is long (96 mm), very low (8 mm high) and of constant height throughout its length. The PDL has a prominent dorsal corner as in the corresponding plate of *Grenfellaspis*, or the mixilateral of *Bothriolepis*. The sutures between plates of the lateral wall are well seen in V.5076.1b (Fig.25B). The plates are preserved in natural association, and both dorsal and ventral margins of the lateral wall

Fig.24. *Xichonolepis qujingensis* P'an & Wang; Zhaojiazhuang near Wuding, Yunnan Province, South China. M. Devonian, dorsal wall of trunk armour, dermal surface, V.5076.1b. Specimen figured in Zhang (1980, pl.1, fig.2). Latex cast whitened with ammonium chloride (x0.6).

are continuous. It is clear from this specimen that *Xichonolepis* had no independent PL plate.

The isolated trunk armour plates include five AMD plates ranging in length from 41 to 103 mm. B/L index increases with size (Table 5). V 5076.1a and 5077 are two larger examples showing the inner surface, with a clear supranuchal area, strong postlevator thickening, but rather indistinct postlevator crista (Figs 25A,26B). The median ventral ridge and groove are well developed (Fig.26A,B). In the smallest specimen (V 9058, Fig.26C) the supranuchal area, postlevator crista and median ventral groove are poorly developed, which may reflect immaturity. The AMD shows the same overlap relations to the dorsolateral plates as in *Grenfellaspis*, with the anterolateral margin overlapping the ADL and the posterolateral margin overlapping the PDL (also seen in asterolepids except *Remigolepis*, and possibly the primitive condition). The AMD has only a median overlap area for the PMD in V 5076.1b, and other specimens showing the visceral surface (e.g., V 9057.8, Fig.26A) show no contact face for the PMD on the posterolateral projections, indicating a non-overlapping lateral section of the posterior margin, as described above for *Grenfellaspis*.

The PMD is narrow and long (B/L index about 66), and the articulated specimen shows it is only slightly shorter than the AMD in the dorsal wall. Its anterior margin is broad and convex, but with a slight median concavity. The lateral margins are gently convex (Fig.26D,E). The PMD overlaps all adjacent plates, as

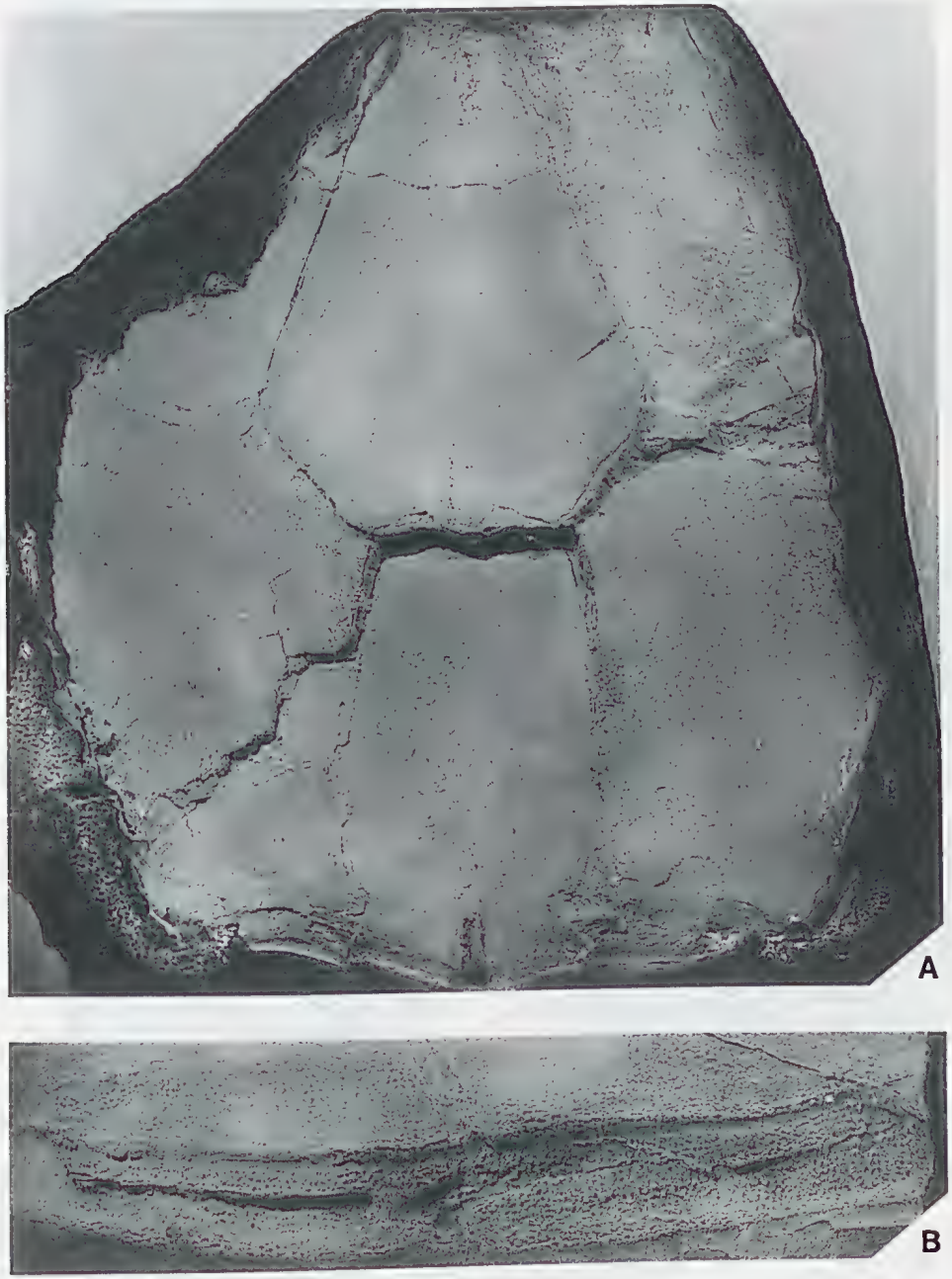

Fig.25. *Xichonolepis qujingensis* P'an & Wang; Zhaojiazhuang near Wuding, Yunnan Province, South China. M. Devonian. A - dorsal wall of trunk armour, visceral surface, V.5076.1a. Specimen figured in Zhang (1980, pl.1, fig.1). Latex cast whitened with ammonium chloride (x0.7). B - right lateral wall of trunk armour, V.5076.1b (*cf.* Fig.24), in lateral view (x0.9).

in all other known antiarch genera. The overlap area for the PDL is narrow but the bone is rather thick. There is only a slight overlap or the PMD may form a butt joint with the PDL. Lateral processes are very strongly developed, but otherwise the PMD is of similar breadth throughout its length, and just slightly narrower anteriorly. The posterior margin is convex, but lacks a posterior corner (Fig.30). The PMD is thus different in shape to that of *Grenfellaspis* (and *Sinolepis*; see below), and most closely resembles the PMD of *Dayaoshania*. The visceral surface as exposed on V 2965.1, 2 shows the median ridge very well developed from the anterior margin backward (Fig.26D,E). Posteriorly it broadens to form a groove, but in the larger V 5076.2a there is an anterior groove and posterior ridge, and in V 5076.1a a shallow groove extends from the posterior division of the AMD across the PMD (Fig.25A), so these structures are variably

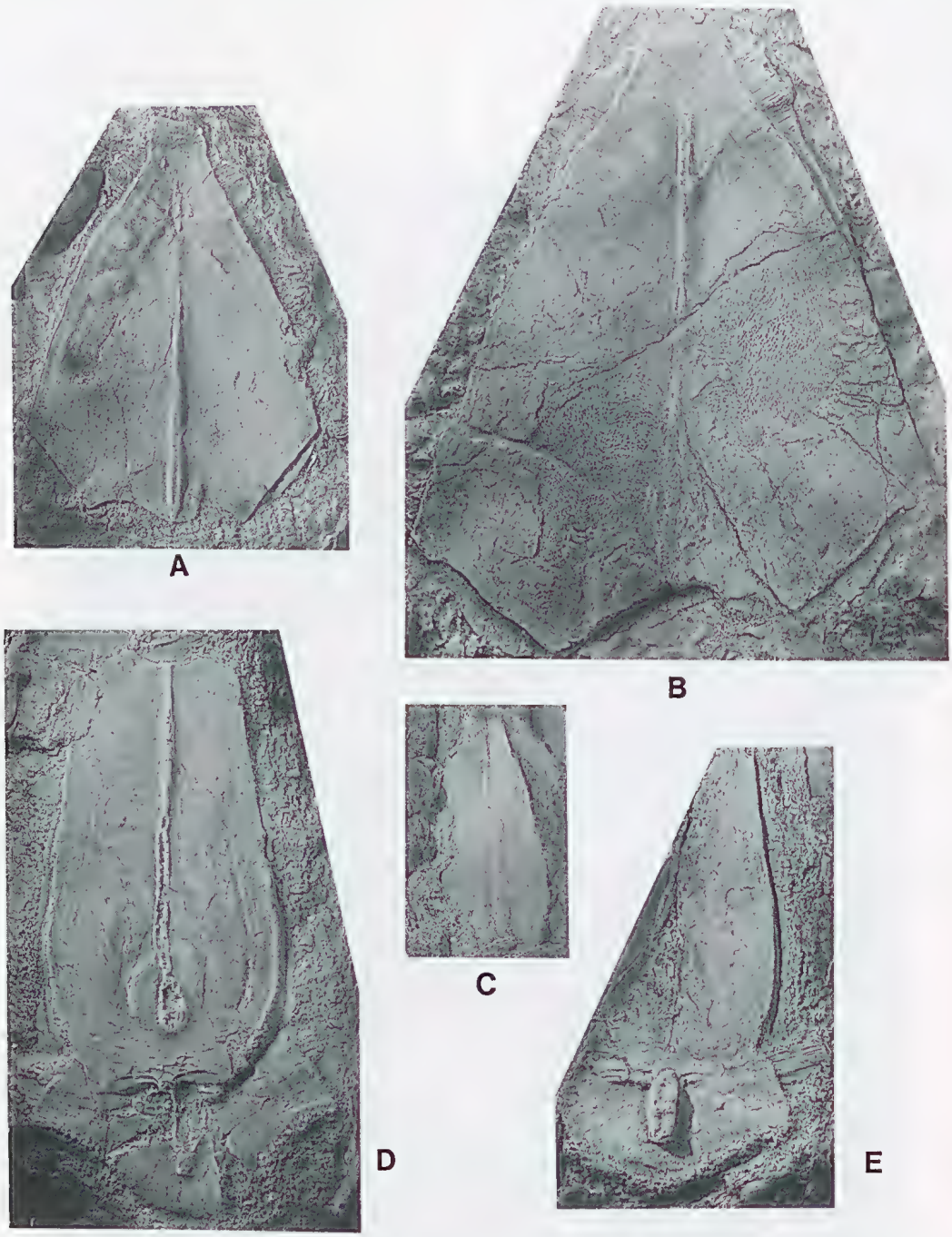

Fig.26. *Xichonolepis qujingensis* P'an & Wang; Middle Devonian, Devonian, Yunnan Province, South China. Median dorsal trunk plates, some of which were figured by Zhang (1980) as indicated below. Plaster casts whitened with ammonium chloride. x0.8 natural size. A-C - anterior median dorsals (AMD), visceral surface. A - V.9057.8; (Wuding, Yunnan). B - V.5077 (1980, pl.2, fig.5); (Qujing, Yunnan). C - V.9058; (Wuding, Yunnan). D,E - posterior median dorsals (PMD), visceral surface. D - V.2965.1 (1980, pl.2, fig.1); (Wuding, Yunnan). E - V.2965.2 (1980, pl.2, fig.2); (Wuding, Yunnan).

developed. The posterior marginal area is relatively long, and the posterior ventral pit and process are placed behind the crista near the posterior margin, and thus in a similar position to that of *Grenfellaspis* (except that in the latter the crista is much broader, and includes the pit). The state of this character is unknown in *Dayaoshania* and *Sinolepis*.

The ADL plate was previously known from V 5076.1, but two new specimens (V 9056.1 and 9057.4) provide more information on the visceral surface. The better specimen (V 9057.4, Fig.27A) is very flat, longer (60 mm) than broad (B/L index 60), and quadrilateral in shape. There is no clear division between dorsal and lateral laminae. The cit is broken laterally but shows normal development. The dorsomesial margin is overlapped by the AMD as already described. The overlap area along the posterior margin is narrow, and lacks the posterior corner seen in bothriolepids. The ventral margin shows an oblique surface, presumably a contact for the AVL, although the main overlap area must have been on the external surface (not known), as in other antiarchs including *Grenfellaspis* described above. Posteroventrally is a short margin which formed a contact with the PVL, and shows that the AVL and PDL were separate. The same arrangement occurs in V 5076.1, and may be developed in some bothriolepids (e.g., variably present in *B. canadensis*; Stensiö, 1948).

Two new complete PDL plates are also preserved in visceral view (Fig.27B,C). The PDL has a distinct dorsal corner and dorsomesial process (Fig.30). It is broadest through the dorsal corner, and in shape resembles the PDL of *Grenfellaspis* rather than that of *Sinolepis*. The visceral surface in both specimens is flat, with no differentiation of dorsal and lateral laminae, and no contact faces developed for overlapping

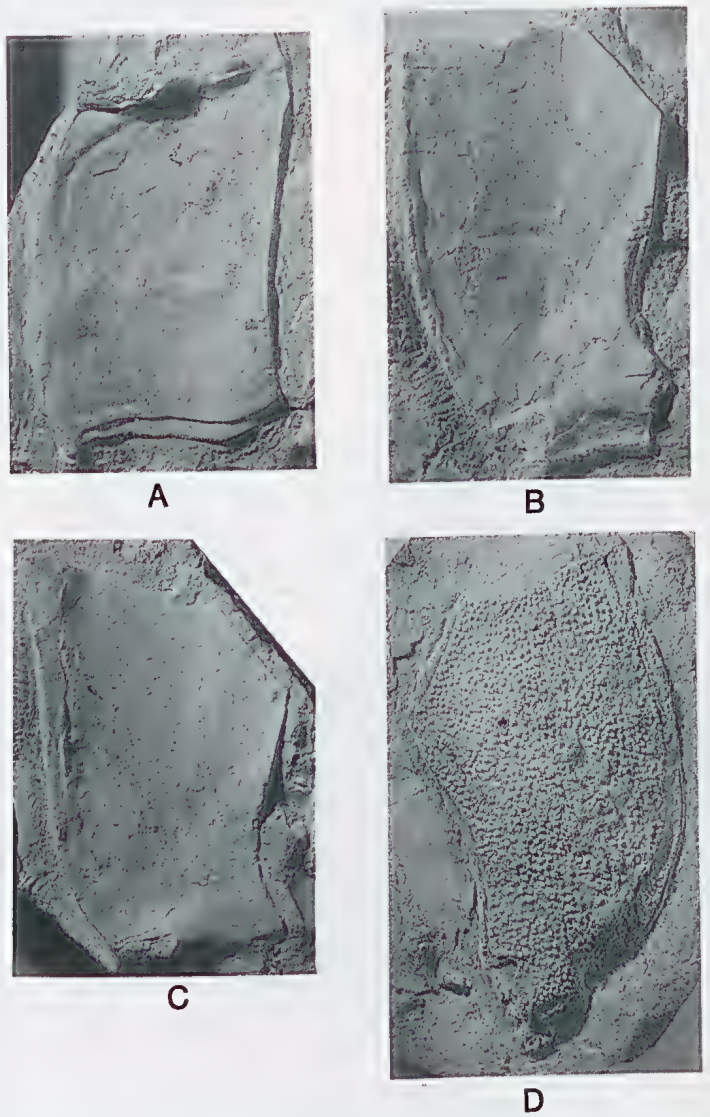

Fig.27. *Xichonolepis qujingensis* P'an & Wang, Middle Devonian, A-C - near Wuding, Yunnan Province, South China; D - from Panxi, near Huaning, Yunnan Province, South China. A-C - dorsolateral trunk plates, visceral surface. Original specimens, uncoated. x0.8 natural size. A - right anterior dorsolateral (ADL), V.9057.4; B - right posterior dorsolateral (PDL), V.9057.2; C - right posterior dorsolateral, V.9057.1. D - right posterior dorsolateral, V.4442.14b (Zhang 1980, pl.3, fig.4). Latex cast whitened with ammonium chloride (x1).

adjacent plates. V 4442 (Fig.27D) is a right plate showing the flat external surface, which lacks a dlr, and has a narrow overlap area along its lateral margin for the PVL. The lateral line groove runs just inside this margin. Since in the somewhat larger V 5076.1 the dlr is clear, its absence is assumed to be a juvenile characteristic in *Xichonolepis*. Two complete examples of the PDL have similar proportions (V 9057.1, 4442.14; length 77 and 70.5 mm, B/L indices 57, 58).

New information on the ventral wall of the trunk armour is provided by several specimens (Fig.29). V 9057.7a,b is part and counterpart of a large right AVL showing most of the inner surface of the bone (9057.7a), with the counterpart displaying the external surface of the lateral lamina and its dorsal margin. Posteriorly the contact face for overlapping the PVL is clearly preserved (Fig.29B), and is longer mesially than laterally, with a distinct mesial ridge just as described above for *Grenfellaspis*. In addition the specimen includes the subcephalic division showing some structures of the brachial articulation. V 9057.7a (Fig.29C) shows the dorsal aspect of a rounded process lying anterolateral to the ventral margin of the foramen axillare, and thus corresponding to the structure in *Grenfellaspis* labelled co.v in Figures 11 and 12. On the counterpart (V 9057.7b) the dorsal margin of the axillary foramen is not well preserved but the foramen seems to be longer than high, and possibly of triangular shape as in *Grenfellaspis*. Above the foramen the concave dorsal surface of the fossa axillaris extends up to the dorsal corner of the AVL (not preserved). The rest of the processus brachialis, fossa articularis pectoralis, and funnel pit are not preserved. Behind the prepectoral corner is a smooth margin 8 mm long which must be the ventral margin of the axillary foramen. The prepectoral corner is not completely preserved. Behind the brachial articulation an obtuse angle is clearly preserved between lateral and ventral laminae of the plate. V 9057.7b shows the dorsal margin of the lateral lamina of the AVL to be fairly straight, and slightly higher at its anterior end. It is about 110 mm in length but only 10.5 mm high. The contact with the ADL is not clear, but presumably the AVL overlapped the ADL as in other antiarchs.

V 5076.6 (Fig.28) is a complete cast of the subcephalic division of the trunk armour, previously figured by Zhang (1984). It is 150 mm wide, with a length of 57 mm, so it came from a large individual. The prepectoral corners are well developed, and the right AVL overlapped the left as in all known antiarchs except yunnanolepids. The semilunar notch is large (81 mm across, 42 mm deep), occupying over half the total breadth of the subcephalic division. We consider therefore that *Xichonolepis* probably possessed paired semilunar plates, as known in *Dayaoshania*, but they must have been much larger than in that form, and of comparable size to those of *Grenfellaspis*. Both sides show a short free margin leading to the anterolateral corner of the AVL (poorly preserved), of similar shape to this region in *Grenfellaspis*. The transverse posterior margin to the subcephalic division in this specimen demonstrates that *Xichonolepis* had a similar morphology of the ventral trunk armour to that described above in *Grenfellaspis*. However, the narrow posterior part of the AVL plates have been broken off this specimen. On the left plate is an unornamented notch, corresponding to the similar structure in *Grenfellaspis* (a.un, Fig.11A).

Another specimen collected in 1962 from Wuding and previously difficult to interpret can now be understood in the light of the new information provided by *Grenfellaspis*. V 2965.7 is a long narrow strip of bone with a convex lateral and concave mesial margin, some 218 mm in preserved length and 23 mm across (Fig.29A). Both ends of the specimen are missing, but it is now clear that this represents the ventral laminae of an AVL and PVL in natural association, which from the overlap relationship must

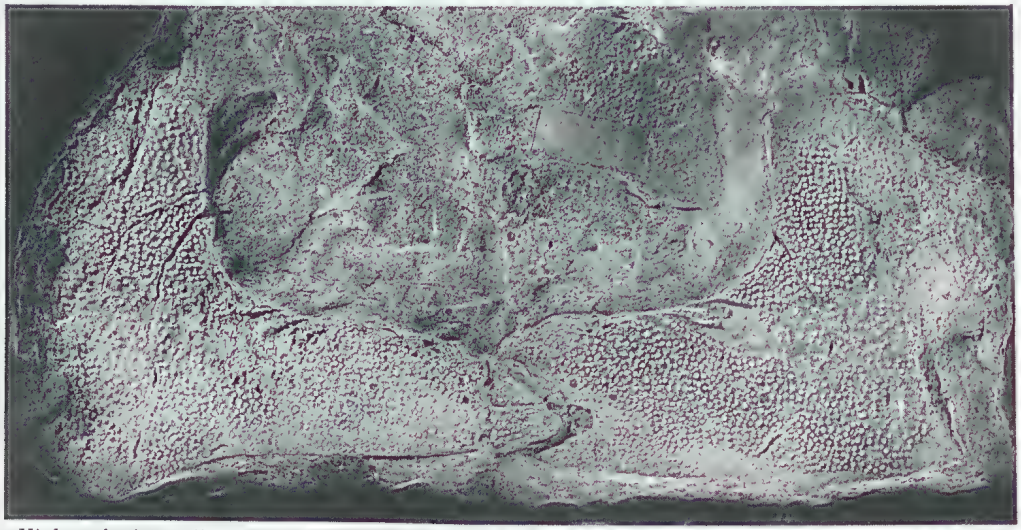

Fig.28. *Xichonolepis qujingensis* P'an & Wang; near Wuding, Yunnan Province, From below Haikou Formation, Middle Devonian. Anterior portion of ventral trunk shield, showing right and left AVLs in association (right overlaps left) and semilunar notch. V.5076.6. Latex cast whitened with ammonium chloride, from impression figured by Zhang (1980, pl.3, fig.1) (x0.8).

be from the left ventrolateral wall of the trunk armour.

V 9057.3 (Fig.29D) is the ventral lamina of a right PVL showing the visceral surface, and complete except for its anterior end. No posterior overlap is seen for the left PVL, but in all known antiarchs the right PVL is normally overlapped by the left, so this would not be seen on the inner surface. The subanal division is short, and shows the posterior margin of the trunk armour to have been concave (Fig.31), as in the other genera described above. However, the lateral subanal process described above in *Dayaoshania* is less pronounced in *Xichonolepis*. The process in this specimen displays a dorsally facing ornamented area extending mesially as a narrow strip inside the posterior margin (Fig.29D). This shows that the tail of *Xichonolepis* must have been much narrower than the trunk armour. The lateral lamina of this specimen

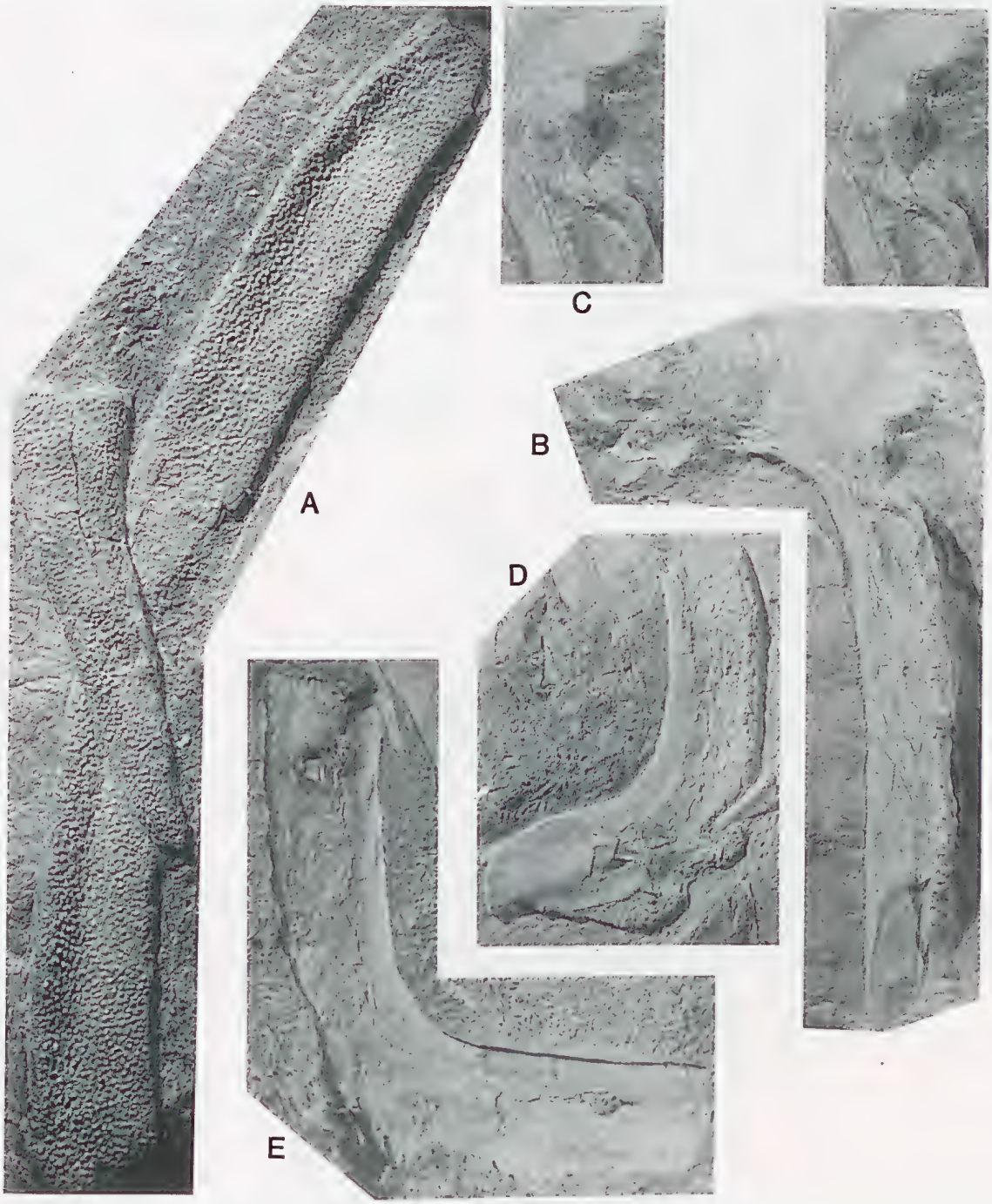

Fig.29. *Xichonolepis qujingensis* P'an & Wang; from near Wuding, Yunnan Province, South China. Middle Devonian. Ventral trunk plates (AVL,PVL). Original specimens. x0.8 natural size. A - associated right anterior (AVL) and posterior (PVL) plates (V.2965.7), partly overlain by the distal segment of a *Xichonolepis* pectoral fin (V.2965.8); B - right anterior ventrolateral, ventral view, V.9057.7a; C - detail of brachial area in V.9057.7a (stereo pair); D - right posterior ventrolateral, V.9057.3, dorsal view. E - left posterior ventrolateral, V.9056, dorsal view.

is broken off, but outside the broken edge is another dorsally facing ornamented surface, which indicates that the rim around the ventral wall in V 5076.1b is not an artefact of preservation. This rim is formed from the expanded ventrolateral ridge of the trunk armour. A second possible PVL (V 9056.2) is from the left side, but only the mesial margin is well preserved (Fig.29E).

P'an & Wang (1978, pl.33, fig.6) figured an incomplete Ml2 from the pectoral fin of *Xichonolepis*, and the only new pectoral fin specimen is a distal segment associated with the left ventral wall of the trunk armour just described (Fig.29A). From their relative sizes and closely similar ornament these associated remains are clearly conspecific and probably come from the same individual. The pectoral fin segment is complete except for the articular region at the proximal end which is slightly broken. It is 84 mm long and 20 mm wide proximally, and slightly curved with a flat exposed surface. In its broad and robust development it is very different from the elongate distal segment of the fin of *Bothriolepis*, or the associated *Dianolepis*. The sutures between bones cannot be traced, so it is not possible to decide whether the dorsal or ventral surface is exposed, and whether the segment comes from the left or right side. It is displaced relative to the associated trunk remains because the distal end points anteriorly towards the AVL plate (Fig.29A).

As previously described (Zhang, 1980), the ornament of *Xichonolepis* is of crowded stellate tubercles, with no obvious alignment into rows. It is difficult to distinguish from the ornament of the associated bothriolepidoid *Dianolepis*.

Sinolepis Liu & P'an, 1958

Emended diagnosis. Headshield large, subrectangular, as long as trunk armour; premedian plate with very short anterior division; postpineal and nuchal plates overlap lateral plate. Trunk armour broad, short, widest anteriorly, tapering posteriorly. Anterior median dorsal plate broad and quadrangular with straight anterolateral and short posterolateral margins. Posterior median dorsal shorter and narrower than AMD. Anterior dorsolateral plate as long as AMD. Subanal margin of ventral trunk wall straight. Pectoral fin as long as trunk armour.

Remarks. The diagnosis presented by Liu & P'an (1958) has been amended in the light of new information

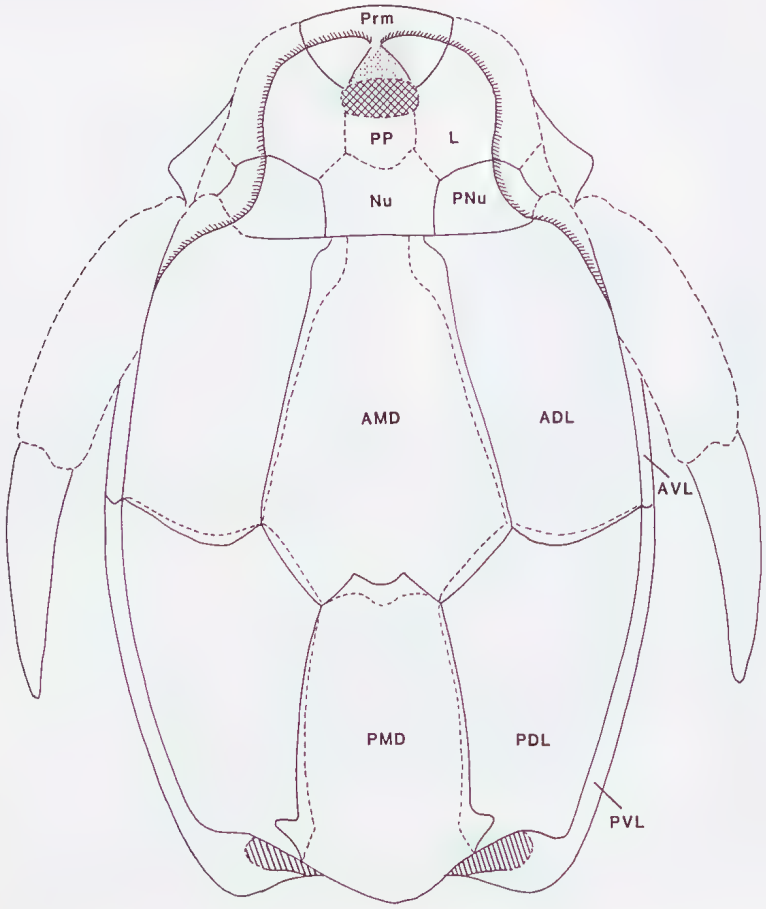

Fig.30. *Xichonolepis qujingensis* P'an & Wang, Middle Devonian, Yunnan Province, China. Reconstruction of armour in dorsal view (approximately two thirds natural size).

provided by the above descriptions. The characters used here are discussed below in the section on sinolepid inter-relationships.

Sinolepis macrocephala Liu & P'an, 1958

Figs 32,33C

Type material. HOLOTYPE, L41-4 (Liu & P'an, 1958, pl.1; pl.4, fig.1).

Other material. Material referred to this species was listed by Liu & P'an (1958).

Type locality. Luntan, near Nanjing, in the lower Yangtze Valley, Jiangsu Province (see Fig.1).

Horizon and age. Wutung Series (Late Devonian, Famennian).

Diagnosis. A *Sinolepis* with a maximal head shield length of about 65 mm, with a B/L index ranging between 100-120, and decreasing with size. AMD with straight anterior margin. Tubercular ornament partly replaced by anastomosing ridges.

Remarks. Three species of *Sinolepis* have been named: *S. macrocephala* (the type species), *S. wutungensis* Liu & P'an, 1958, and *S. szei* Pan *et al.*, 1987. *S. wutungensis* was based on a single small AMD plate from the type locality which was said to differ from the type species in being broader than long, with a concave anterior margin and less distinct median dorsal ridge (Liu & P'an, 1958: 40). More material is required to confirm the validity of this species. *Sinolepis szei* from the Upper Devonian of Ningxia was diagnosed by its large size (head shield 106 mm long), with an elongate postorbital part of the head shield (Pan *et al.*, 1987: 184). Like *S. wutungensis*, the AMD has a concave anterior margin, but it was evidently of more elongate proportions (Pan *et al.*, 1987, fig.48). Large size in itself is not a convincing difference, since the type species is known from only one collecting site, where most specimens collected are much smaller, and of similar size. However the largest known skull of *S. macrocephala* (Liu & P'an, 1958, pl.5, fig.1; the paratype, length about 63 mm) has more elongate proportions (B/L index about 104) than smaller specimens (B/L index up to 120; Liu & P'an, 1958: 31), suggesting a decrease in B/L index with size

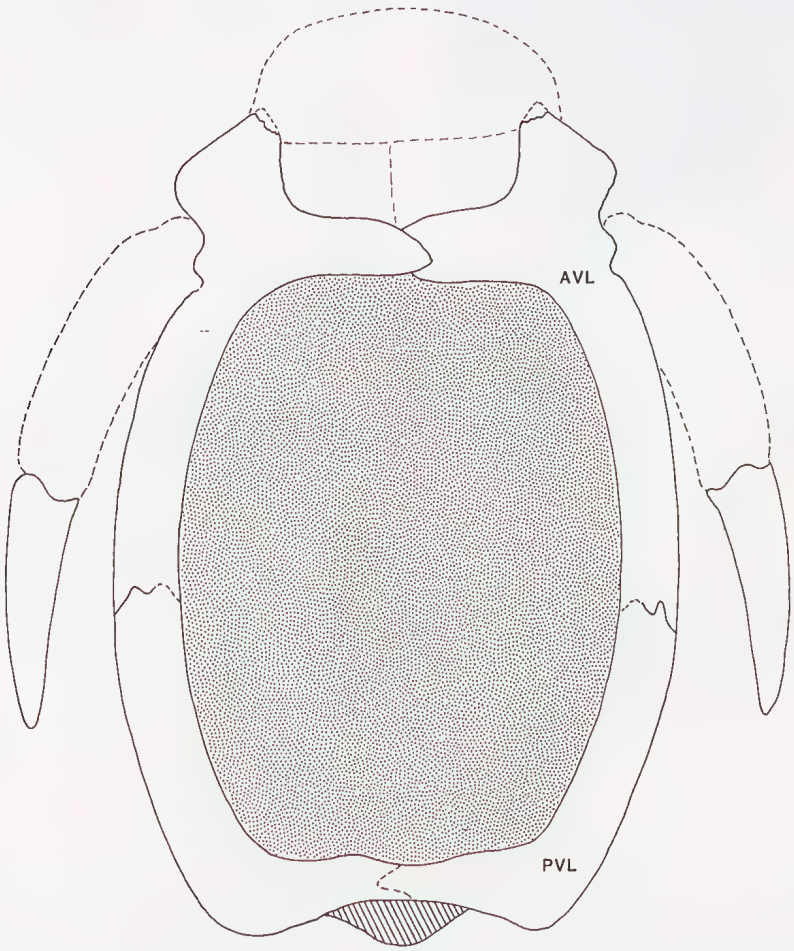

Fig.31. *Xichonolepis qujingensis* P'an & Wang, Middle Devonian, Yunnan Province, China. Reconstruction of armour in ventral view (approximately two thirds natural size).

as included in the above diagnosis. In contrast the larger more coarsely ornamented skull of *S. szei* has a greater B/L index (about 138), and although based on a single specimen this difference in proportion suggests that it is a valid species.

New interpretations presented below are all based on the type species, *S. macrocephala*.

Description. The type collection includes two nearly complete articulated individuals preserved in dorsal view, two other fishes with head and trunk preserved, and a few isolated plates, and was fully described and figured by Liu & P'an (1958). Here we comment on some problematic aspects of morphology arising from the above descriptions of *Grenfellaspis*, *Dayaoshania*, and *Xichonolepis*. One specimen (L41-10) showing the AVL plate from the trunk armour is redescribed, and the structure of the pectoral fin is reinterpreted.

New restorations of the skull of *Sinolepis* have been presented by Long (1983), Young (1984c), and Pan *et al.* (1987). The most significant change from the original reconstruction is the long obstantic margin with an anteriorly placed PM plate, which gives the skull a hexagonal shape similar to that of bothriolepids and yunnanolepids, rather than asterolepids (Fig.33). The former condition is regarded as primitive for antiarchs generally (Young, 1984c). *Sinolepis* resembles *Grenfellaspis* in various skull features, for example the broad shallow grooves for the sensory canals.

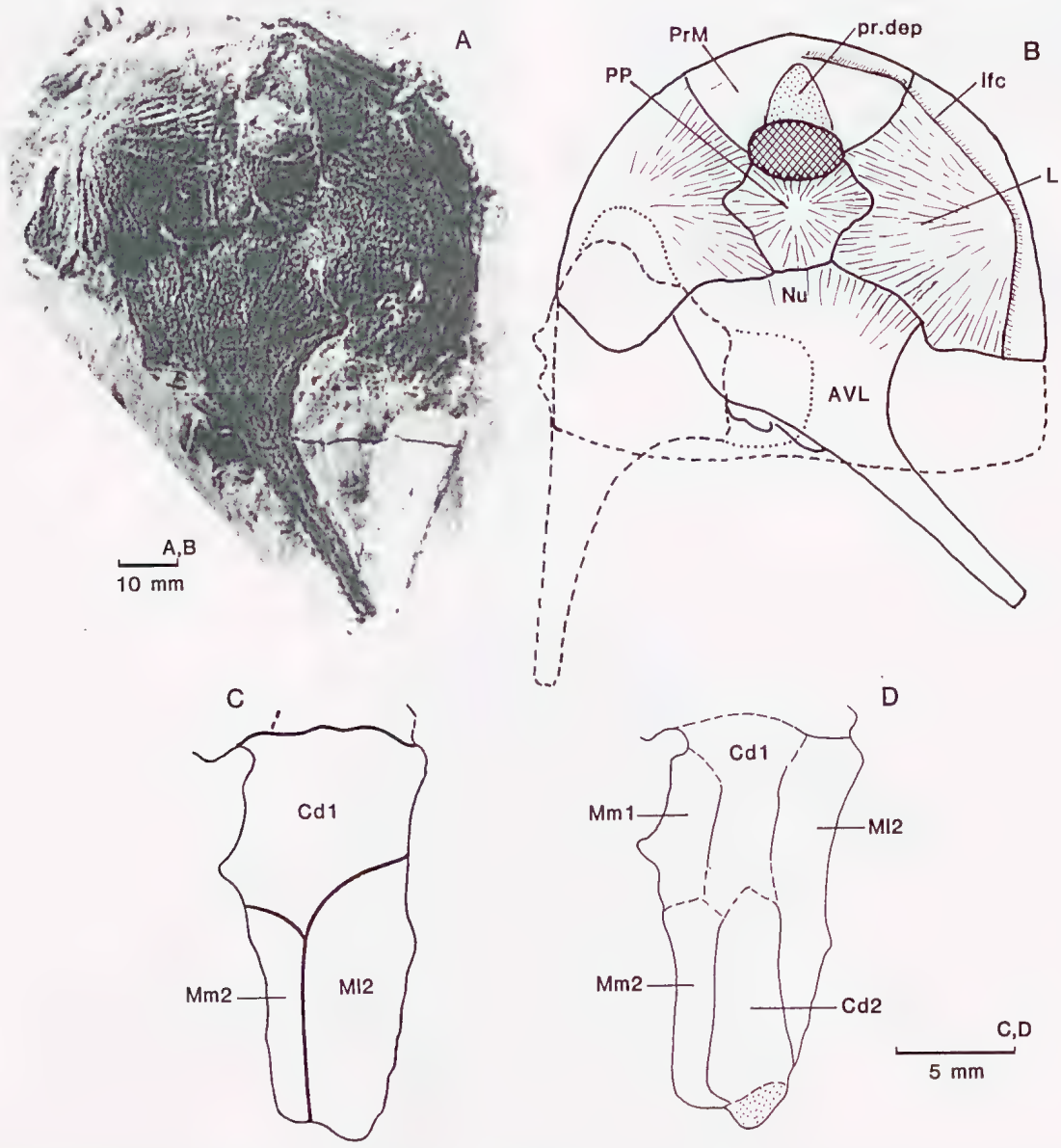

Fig.32. *Sinolepis macrocephala* Liu & P'an. A - headshield and right AVL, in ventral view. (specimen no. L41-10, refigured from Liu & P'an, 1958, pl.VII, fig.2b) B - reinterpretation of same specimen with original position of displaced AVL indicated by broken line; after information from *Grenfellaspis*, *Xichonolepis* and *Dayaoshania*. C - Liu & P'an's (1958) interpretation of the pectoral fin in specimen no. L41-6 (1958, pl.2). D - new interpretation of pectoral fin, traced from Liu and P'an's illustration, but based on new information from the pectoral fins of *Dayaoshania* and *Grenfellaspis*.

The ventral wall of the trunk armour was one aspect of the morphology of *Sinolepis* on which the type material provided little information. Liu & P'an (1958: 34,36) noted the presence of a clearly defined rim around the edges of the trunk armour as preserved in the holotype and paratype, which suggested that the ventral wall was probably broader and longer than the dorsal wall. A similar condition was described above for *Xichonolepis*. The long and low lateral laminae of the AVL and PVL plates were identified on the holotype (Liu & P'an, 1958, pl.1), but no other information was provided on the ventral wall, because both specimens are preserved in dorsal view.

In a re-examination of the material in 1981 it was discovered that another specimen described and figured as showing the anterior part of the headshield (Liu & P'an, 1958: 32, pl.7, fig.2) includes a displaced right AVL. In view of the highly unusual shape of the AVL and PVL plates in the three genera described above, it is not surprising that the AVL was not recognised in the original description of this specimen as an element of any significance. Without the benefit of comparative material of *Grenfellaspis* as described above, the elongate projection behind the small head-shield in specimen L41-10 has the appearance of a very incomplete fragmentary plate (Liu & P'an, 1958, pl.7, fig.2). This specimen (Fig.32A) demonstrates conclusively that the AVL of *Sinolepis macrocephala* was developed essentially as in *Grenfellaspis*, *Dayaoshania* and *Xichonolepis*. The much reduced ventral lamina is represented only by a mesially directed transverse process (pr.tr) which was in contact with its antimere in the region of the crista transversalis interna anterior, and a narrow posterior process (pr.p) representing the ventrolateral ridge of the trunk-armour. However, the transverse process is somewhat broader than in *Xichonolepis* or *Grenfellaspis* (Figs 17,31). The semilunar notch is poorly seen but evidently of similar size and shape to that of *Grenfellaspis* or *Xichonolepis*. Incomplete remains of the brachial process (pbr) are also seen inside the prepectoral corner (prc).

Pan *et al.* (1987, fig.49) attributed an incomplete right AVL and associated pectoral fin to their new species *Sinolepis szei*, but, as preserved, this specimen has a more typical antiarch morphology and, on the evidence presented above, cannot belong to *Sinolepis*. The elongate pectoral fin suggests instead that it may belong to a bothriolepid antiarch. The fin itself is too poorly preserved to reveal details of suture pattern.

The suture pattern on the pectoral fin of *S. macrocephala* as originally restored by Liu & P'an (1958) has been of central importance in all previous considerations of the relationships of the genus. In their restoration in dorsal view (Liu & P'an, 1958, fig.5) the fin was shown to resemble that of *Bothriolepis*, with lateral and mesial marginal plates in contact with an extensive suture, and widely separating first and second dorsal central plates. It was noted that 'at the distal end

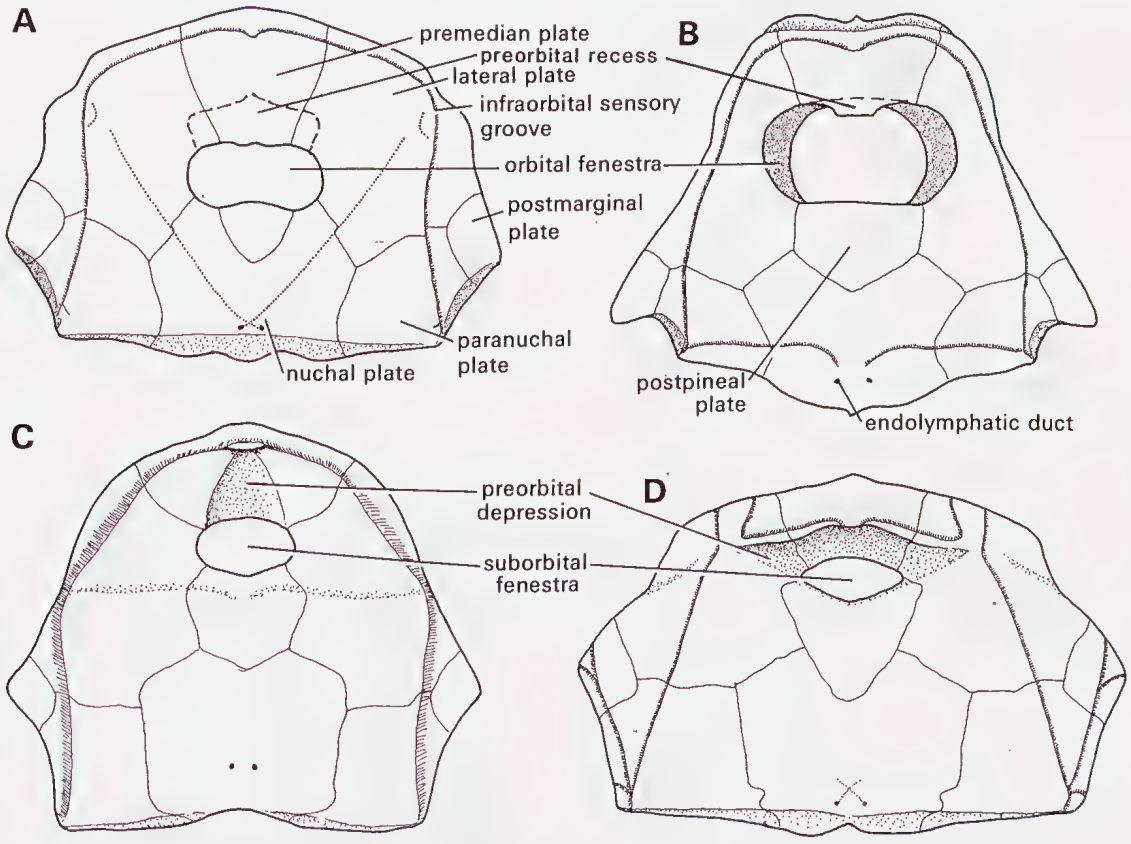

Fig.33. Skull roof patterns of representatives of the four major antiarch subgroups. Not to scale. (modified after Young 1984, fig.1) A - *Bothriolepis* (after Stensiö, 1948); B - *Asterolepis* (after Karatajute-Talimaa, 1963); C - *Sinolepis* (after Liu & P'an, 1958; Long, 1983); D - *Yunnanolepis* (after Zhang, 1978)

there is probably a small plate corresponding to the Cd2 of *Bothriolepis*, but being too ill-defined, a description of it is superfluous' (Liu & P'an, 1958: 34). Largely based on this description of the pectoral fin, and its similarity to that of bothriolepids, the sinolepids were placed as a sister group to bothriolepidoids in the phylogenetic scheme of Young (1984c).

The description of Liu & P'an (1958) is at variance with the structure of the pectoral fin as described above in *Grenfellaspis* and *Dayaoshania*, but from the published figures an alternative interpretation of the fin of *Sinolepis* can be suggested. Bone sutures are most clearly seen in the specimen illustrated by Liu & P'an (1958, pl.2), which shows the proximal part of the pectoral fin on the right side, with the elements labelled Cd1 and Ml2 clearly confined only to the central part of the dorsal surface of the fin. The large lateral element must be the Ml2 (Fig.32D), but the distal half of the preserved portion has two clear longitudinal sutures, not a single one as interpreted by Liu & P'an (1958). These sutures surely delineate an elongate Cd2 reaching proximally to meet with the Cd1, as described above in *Dayaoshania*. Along the mesial margin of the preserved portion two plates can be inferred. A well defined suture shows a dorsal lamina of the Mm1 attached to the Cd1, just as in *Dayaoshania* and inferred for *Grenfellaspis*. Preservation is less clear on the holotype of *Sinolepis*, but the more incomplete left fin Liu & P'an (1958, pl.1) suggests a Cd1 similarly restricted to the central part of the dorsal fin surface. We suggest therefore that restudy of the material of *Sinolepis* will reveal a pectoral fin structure essentially the same as that described above for *Grenfellaspis* and *Dayaoshania*.

Discussion

Inter-relationships of sinolepids. Of the many morphological characters dealt with in the above descriptions, those relevant to a consideration of the interrelationships and relationships of sinolepids are further discussed here. Distribution amongst the various antiarch subgroups of characters proposed as synapomorphies in the cladograms of Figure 34 are summarised in a data matrix in Table 6. (A new sinolepid genus, *Vanchienolepis*, was recently erected by Tong-Dzuy & Janvier, 1990; it clearly belongs to the Sinolepidae on the evidence of the trunk armour, but has not been included in this discussion. The skull and pectoral fin are unknown.)

As will be seen from this matrix, the condition of many characters for many taxa is unknown. These gaps in knowledge are inevitable when dealing with incompletely preserved fossil taxa. As discussed by Zhang & Young (1992), such gaps prevent any rigorous parsimony analysis, unless unknown character states are incorporated as predictions of the preferred cladogram. However, the data matrix serves as a guide for future research in two ways: as a summary of known and predicted character distributions within the context of a preferred phylogeny; and to focus collecting effort on reducing the proportion of missing character states for the group in question.

Antiarchs were highly specialised fishes, and for some characters, for example those concerned with the dermal pectoral articulation (a unique condition amongst vertebrates), decisions regarding character polarity are clear cut. Similarly, the major antiarch subgroups are supported by a number of good synapomorphies, and areas of disagreement in the current literature mainly concern structures for which we lack information in some of the taxa in question. Current phylogenetic schemes for placoderms generally (e.g., Young, 1986) and antiarchs as a major placoderm group (e.g., Janvier & Pan, 1982; Long, 1983; Pan *et al.*, 1987; Young, 1984c, 1988a), provide a phylogenetic framework for interpreting the new characters or character combinations arising from the above descriptions. Arguments supporting character polarity, mainly using outgroup comparisons, are given below for each of the 11 characters used in this analysis. The two instances of homoplasy in the analysis are also commented on below (for characters 1,2).

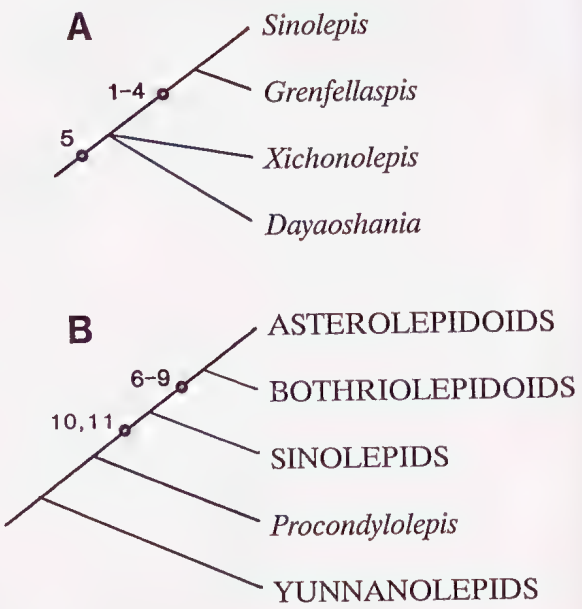

Fig.34. A - scheme of inter-relationships of sinolepid genera; B - suggested relationships of sinolepids to other major antiarch groups. Characters 1-10 as follows: 1 - lateral position of ifc on PNu and La, forming narrow lateral divisions; 2 - broad anterior margin to AMD; 3 - short posterolateral margin of AMD; 4 - square shape of PMD, with reduced lateral processes; 5 - large rectangular aperture in ventral trunk wall; median ventral plate absent; AVL and PVL reduced to narrow ventral laminae; 6 - Cd1 and Cv1 have large semicircular articular areas, similar in size and closely integrated to ornamented part of bone; 7 - mesial lamina on Cd1; 8 - Mm1 restricted to mesial wall of pectoral fin; 9 - brachial articulation with large, helmet-shaped processus brachialis; 10 - distal joint of pectoral fin; 11 - nerves and vessels to pectoral fin passing through a single axillary foramen.

First, various similarities observed in the above descriptions of the four sinolepid taxa may be separated into symplesiomorphies and synapomorphies. The genera *Dayaoshania* and *Xichonolepis* resemble each other in the following characters not seen in *Grenfellaspis* or *Sinolepis*: a) the broad lateral division on the paranuchal and lateral plates; b) the elongate anterior division of the premedian plate; c) the shape of the anterior median dorsal plate, with a narrow anterior margin, and pronounced lateral corners; d) the shape of the posterior median dorsal plate, with pronounced lateral processes. However, outgroup comparisons suggest that these are symplesiomorphies, because they also occur in other antiarch groups which on other evidence are monophyletic (e.g., a + b in yunnanolepids and bothriolepids; c in yunnanolepids and asterolepids).

Sinolepis, *Xichonolepis* and *Grenfellaspis* resemble each other, and differ from *Dayaoshania*, in having a deep semilunar notch and large apparently paired semilunar plate. By outgroup comparison this is also regarded as a symplesiomorphy, being seen in yunnanolepid and asterolepid antiarchs.

There are no obvious similarities of *Xichonolepis* and *Sinolepis* to the exclusion of the other taxa. However *Grenfellaspis* and *Sinolepis* resemble each other in several features which are possible synapomorphies (numbered as in Fig.34A): **1**) lateral position of the infraobital sensory groove on the paranuchal and lateral plates, giving these bones narrow lateral divisions; **2**) broad anterior margin to the anterior median dorsal plate; **3**) short posterolateral margin of the anterior median dorsal; **4**) square shape of the posterior median dorsal plate, with reduced lateral processes.

We interpret the lateral position of the infraobital sensory groove to be specialised, because the sensory groove arrangement which results in the broad lateral division in *Yunnanolepis* (Fig.33D) is also primitive in pattern, by comparison with an outgroup such as arthrodires. In addition *Yunnanolepis* is the most primitive known antiarch in several other major respects (e.g., pectoral fin articulation) although it is acknowledged that primitiveness in one feature does not necessarily imply primitiveness in another. Our interpretation predicts that the paranuchal and lateral plates of *Procondylolepis*, when described, will have narrow lateral divisions, and requires that the lateral position of the groove in asterolepidoids (Fig.33B) is independently acquired.

Similarly, character 2 is interpreted as independently acquired in bothriolepidoids and the two youngest sinolepid genera, because a narrow anterior margin to the anterior median dorsal plate occurs in the primitive *Yunnanolepis*. This argument is not supported by any clear-cut outgroup comparison, because other placoderm groups have both broad and narrow median dorsals. However, the fact that all known Early Devonian antiarch taxa, and most Middle Devonian taxa, have a narrow anterior division, provides a biostratigraphic argument in support of the interpretation adopted here. Characters 3 and 4 are regarded as specialised by outgroup comparison with other antiarchs, since the alternative interpretation is less parsimonious in requiring independent loss of this character in *Xichonolepis* and *Dayaoshania*, yunnanolepids, and the common ancestor of bothriolepidoids and asterolepidoids. The validity of this argument depends on the monophyly of the Sinolepidae, discussed next.

Young (1984c, fig.2) proposed six possible synapomorphies defining sinolepids as a group, but new evidence now suggests that most of these are probably symplesiomorphies. Only one distinctive character is used here to define the group (Fig.34A): **5**) the large rectangular aperture in the ventral wall of the trunk armour, formed by the much reduced ventral laminae of anterior and posterior ventrolateral plates, and the absence of the median ventral plate.

Since all other placoderms with a long trunk armour (i.e., all other antiarchs, arthrodires, petalichthyids, phyllolepids, etc.) had one or two median ventral plates, and the ventrolateral plates were always developed with extensive ventral laminae, we consider this character to strongly support the monophyly of the Sinolepidae.

Relationships of sinolepids. Earlier views on the relationship of sinolepids to other antiarchs were summarised in the introduction. Most recently Young (1984c, fig.2; 1988, fig.68A) suggested a sister group relationship to bothriolepidoids, whilst Pan *et al.* (1987, fig.51) reiterated an earlier view of Janvier & Pan (1982, fig.12) and Long (1983, fig.11) that sinolepids were the sister group to bothriolepids plus asterolepids. The two synapomorphies of sinolepids and bothriolepidoids proposed by Young (1984c: 446) were: '12) elongation of the proximal part of the pectoral fin, with reduction of dorsal central plate 2 ; 13) PVL and posterior lateral plate fused to form (or replaced by) a single plate (*sensu* Janvier & Pan, 1982)'.

In the light of the new descriptions presented above neither can now be maintained. There is no evidence to support the view that sinolepids had a mixilateral plate, and the simplest explanation of the observed morphology is that they lost their posterior lateral plate with the development of a very low lateral wall to the trunk armour, leaving only the posterior dorsolateral plate. Unlike asterolepids, there is no evidence that the posterior lateral plate was fused to adjacent plates. In the pectoral fin it is now demonstrated that in *Grenfellaspis*, *Dayaoshania*, and presumably *Xichonolepis* and *Sinolepis*, the second dorsal central plate was not reduced as in bothriolepids, but was a large bone of the type seen in asterolepids, this being reasonably considered on morphological grounds to be the primitive condition (Young, 1984a).

That sinolepids are relatively primitive antiarchs is indicated by their retention of the preorbital depression, as in yunnanolepids, a structure which, in euantiarchs, is replaced by the preorbital recess (Janvier & Pan, 1982; Young, 1984c). Thus, in sinolepids, yunnanolepids and other groups with the preorbital depression, the central opening in the skull

is homologous with the suborbital fenestra of advanced antiarchs (Fig.33). The new material also confirms that sinolepids were more primitive than either bothriolepidoids or asterolepidoids in the structure of the brachial articulation and pectoral fin.

From our detailed knowledge of *Grenfellaspis* this genus may be regarded as typifying sinolepids, an assumption corroborated by the more limited evidence currently available from the other three genera. The pectoral appendage of *Grenfellaspis* is regarded as primitive in the following four respects: a) flat shape of the articular processes on the first dorsal and ventral central plates (Cd1, Cv1); b) absence of a dorsomesial crest and mesial lamina on the first dorsal central plate; c) presence of a dorsal lamina on the first mesial marginal plate (Mm1); d) much smaller articulation on the first ventral central plate.

The polarity of these states is based on the pectoral fin of *Procondylolepis*, which is the oldest and least complex armoured pectoral appendage known, with small dermal articulations on both the first ventral and first dorsal central plates. In contrast, the appendage of more advanced antiarchs is characterised by the following (numbered as in Fig.34B): **6**) the first dorsal central ventral central plates have large semicircular articular areas, of similar size and closely integrated to the ornamented part of the bone; **7**) a mesial lamina on the first dorsal central plate; **8**) the first mesial marginal plate restricted to the mesial wall of the pectoral fin.

The pectoral articulation on the anterior ventrolateral plate of sinolepids is also of primitive structure. In *Grenfellaspis* it comprised a triangular dorsal and a small ventral articular area respectively for the first dorsal and ventral central plates of the pectoral appendage, which pivoted around a single axis passing through these articulations. This is very different from the brachial articulation of more advanced antiarchs (bothriolepidoids, asterolepidoids), which possess: **9**) a large helmet-shaped processus brachialis, with the dorsal and ventral articulations developed as deep hemispherical grooves separated anteriorly by the narrow pars pedalis of the brachial process.

A dermal pectoral articulation is not recorded in any other vertebrates, and its greatest complexity is seen in the more advanced antiarchs (bothriolepidoids and asterolepidoids), so both outgroup and complexity arguments support the monophyly of euantiarchs based on character 9. In contrast, in sinolepids there was apparently no pars pedalis, and the anterior edge of the brachial process was continuous with the prepectoral corner of the anterior ventrolateral plate, this presumably representing the primitive condition, by outgroup comparison with *Procondylolepis* (Zhang, 1984). In addition, the sinolepids demonstrate that the complete brachial process appeared after the jointed pectoral fin was acquired.

We consider therefore that there is now ample evidence for placing sinolepids outside the asterolepidoids and bothriolepidoids (euantiarchs), as proposed by Janvier & Pan (1982), but the character they used to support euantiarch monophyly (presence of a 'brachial process') is no longer valid, because a rudimentary process is already present in *Procondylolepis* and sinolepids. Pan *et al.* (1987: 118) proposed that Euantiarchi be extended to include *Procondylolepis*, but the structure of the brachial articulation is very different from that in *Bothriolepis*, *Asterolepis* or *Remigolepis*, where the brachial process is fully formed, and this remains a valid character for euantiarchs in the original sense (and is thus equivalent to the Holocondylolepiformes of Zhang, 1984).

Sinolepids are more advanced than either yunnanolepids or *Procondylolepis* in possessing a distal joint in the pectoral fin (Young & Zhang, 1992). This structure had evolved at least by the end of the Early Devonian, as evidenced by *Liujiangolepis* recently described from Guanxi (Wang, 1987; the ventral armour of this form is not well known but, as described, the ventral armour wall is wider than the dorsal wall and the semilunar may be paired)*. Since the possession of a distal joint is a more complex condition than the unsegmented appendage of *Procondylolepis*, it may be assumed to be the specialised condition, and thus the following is proposed as a synapomorphy supporting a sister group relationship of sinolepids to asterolepidoids plus bothriolepidoids (Fig.34B): **10**) a distal joint in the pectoral fin.

An axillary foramen was previously inferred to have been present in the pectoral fin articulation of *Procondylolepis* (Zhang, 1984). However, a reinterpretation based on new material (Young & Zhang, 1992) now shows that the nerves and vessels to the fin passed through several small foramina, the primitive condition by outgroup comparison with arthrodires. The larger single axillary foramen is seen in only three groups: sinolepids, asterolepidoids and bothriolepidoids. Like Long (1983) therefore, we put forward the following as an additional synapomorphy at this level in the cladogram (Fig.34B): **11**) nerves and vessels to pectoral fin passing through a single axillary foramen.

Biostratigraphy

Middle Devonian. The age of the Dayaoshan Group containing *Dayaoshania* is poorly constrained (Hou, Wang *et al.*, 1989). There are no marine horizons nor any palynological evidence of age in overlying strata which are very poorly exposed beneath Givetian marine beds higher in the sequence. The Dayaoshan Group is primarily a sandstone

* *note added in press*: Further preparation of the specimen figured by Wang (1987, pl.2, fig.3) has recently confirmed that this form is also a sinolepid.

sequence, and is completely unfossiliferous except for the fish horizon (containing *Dayaoshania*) near its top. Its lower part rests unconformably on pre-Devonian rocks. The provisional Emsian-Eifelian age is based on general comparisons of the fish fauna.

Late Devonian. The only detailed consideration of the stratigraphic relationships of the Upper Devonian sediments of the Grenfell area is based on the mapping of J.R. Connolly, who presented a synthesis (1965) of the stratigraphy and correlation of the Hervey Group of central NSW. Connolly (1965, table 1) recognised three major lithological sequences which he formalised as subgroups of the Hervey Group: a lower Beargamil Subgroup of mainly red beds, lithic sandstones and arkoses; a middle Nangar Subgroup mainly comprising a rhythmic succession of white and red sandstones, and an upper Cookamidgera Subgroup, again mainly of red siltstones and shales. Correlation between the three main synclinal belts containing Hervey Group sediments was based primarily on lithological grounds, but also took into account the occurrence of placoderm plates from various localities and horizons (mainly within the sandstones of the Nangar Subgroup), referred to by Connolly as the 'bothriolepid fish assemblage'. This was based on the work of Hills (1932, 1936), who identified the antiarchs *Bothriolepis* and *Remigolepis* in a fish fauna from Gingham Gap in the Hervey Syncline, about 100 km north of the Grenfell area. However, Hills did not formally describe and name these species, and this and most other localities from which fish plates have been recorded remain very poorly known.

In the Grenfell area the Hunter Siltstone containing the *Grenfellaspis* fauna overlies a sandstone unit (the Peak Sandstone) which rests unconformably on Lower Devonian volcanics (Connolly, 1965, fig.11), and these formations were therefore referred to the lowermost Beargamil Subgroup. However detailed work on the vertebrate fauna and on other vertebrate occurrences in the Upper Devonian of NSW, currently in progress, suggests that the Hunter Siltstone is considerably younger than the stratigraphy indicates, and indeed may be one of the youngest Devonian vertebrate faunas known from eastern Australia. A preliminary faunal list is as follows:

antiarchs	*Grenfellaspis branagani* n.sp.
	Bothriolepis sp.
	Remigolepis sp.
arthrodires	*Groenlandaspis* spp.
acanthodian	ischnacanthid jaw bones indet.
dipnoans	cf. *Ctenodus* (Long, 1987: 310)
crossopterygians	porolepiform scales
	?*Eusthenodon* sp.

A noteworthy feature is the absence of phyllolepid placoderms, which occur widely in other Famennian fish faunas in NSW (e.g., Ritchie, 1984). The associated *Groenlandaspis* is a new species with unornamented dermal bones, which also occurs on the south coast of NSW in the Worange Point Formation (Ritchie, in preparation), where again it is associated with antiarchs (*Bothriolepis, Remigolepis*) and crossopterygians (a holoptychiid porolepiform, but with different scale morphology to that from the Grenfell fauna). Phyllolepid remains occur lower in this sequence, but not in the Worange Point fauna (Young, 1983), which suggests that both this and the Grenfell fauna represent a younger horizon than the upper limit of *Phyllolepis*, which occurs in the Famennian of Europe, and is regarded as a reliable index fossil for the late Famennian (e.g., Westoll, 1979; Lelievre & Goujet, 1986; Young, 1988b). The different crossopterygian, and absence of *Grenfellaspis*, suggest that the Worange Point fauna may be slightly older than the *Grenfellaspis* fauna. Evidence from borehole data in western New South Wales suggests that the *Bothriolepis-Remigolepis* assemblage approximates to the *Retispora lepidophyta* palynofloral zone of Playford (1976, 1982), which crosses the Devonian-Carboniferous boundary. Thus an earliest Carboniferous age for the Grenfell assemblage cannot be excluded. Janvier *et al.* (1984) regarded *Groenlandaspis* as also extending possibly into the earliest Carboniferous. This assessment based on the vertebrate assemblages is supported by palynological evidence of the age of the Chinese sinolepid occurrences.

Cai *et al.* (1987) have recently discussed the age and correlation of the Devonian - Carboniferous transitional sequences of south China. Before the discovery of placoderms in the late 1950's the upper part of the Wutung Formation (Leigutai Member) of the lower Yangtze Valley was regarded as Early Carboniferous in age on the evidence of plant macrofossils (e.g., Gothan & Sze, 1933; Sze, 1956). The macroplants include *Leptophloeum rhombicum, Cyclostigma kiltorkense*, and *Archaeopteris* sp. which are associated with the *Sinolepis* fish fauna in the lower part of the Leigutai Member. Pan (1981) placed the *Sinolepis-Asterolepis sinensis* assemblage as the youngest antiarch assemblage known from China, of late Upper Devonian age. In addition the Leigutai has recently yielded abundant miospores in which three assemblage zones have been recognised by Ouyang & Chen (1987): the lower *Retispora lepidophyta-Apiculiretusispora hunanense* (LH) zone (including the fish horizon) is placed in the late Famennian (Fa2d), and the overlying (LC) Zone may be Tournaisian (Tn1a to early Tn1b), although a latest Devonian age is preferred by Cai *et al.* (1987).

This evidence is consistent with that from the upper part of the Sanmentan Formation in Jiangxi Province, where the same *Sinolepis - Jiangxilepis* fish fauna (Zhang & Liu, 1991) is associated with a similar suite of macroplants, and (from the Changyi and Quannan localities in southern Jiangxi) a miospore assemblage including *R. lepidophyta* (Cai *et al.*, 1987). The lower part of the Sanmentan has a marine *Yunnanella* fauna, and the underlying Zhongpeng Formation contains several *Bothriolepis* and macroplant horizons.

In summary, the *Sinolepis* beds of south-eastern China are apparently of similar age to the *Grenfellaspis* fauna of south-eastern Australia. However, *Remigolepis* is apparently absent (although a new remigolepid occurs in the Sanmentan Formation, and *Remigolepis* sp.

is known from Hunan Province) perhaps indicating that the *Sinolepis* beds of south-east China lie above the range of *Remigolepis*. In contrast, *Remigolepis* is known to be associated with *Sinolepis* in north China, but there is other evidence that this fish assemblage may be older. The Middle-Upper Devonian continental sequence in Ningxia Province, and its contained flora and fauna, has been dealt with in an important monograph by Pan *et al.* (1987). From the uppermost Devonian formation, the Zhongning Formation, comes a fish fauna which includes indeterminate galeaspid agnathans and sarcopterygians, six species of *Remigolepis*, and one species of *Sinolepis*. Associated are macroplants including *Leptophloeum rhombicum*, *Sublepidodendron mirabile*, *Eolepidodendron wusihense*, *Sphenopteris taihuensis*, and *Ningxiaphyllum trilobatum*. A miospore assemblage of 20 genera and 32 species includes *Calamospora atava*, *C. nigrata*, *Retusotriletes distinctus*, *Verruciretusispora robusta*, and *Geminospora lemurata*.

The evidence of the plants and spores is cited by Pan *et al.* (1987) in support of a Famennian age for the Zhongning Formation, but the spore assemblage is somewhat different from that listed above for the Wutung Formation. Dr G. Playford (*in litt.*) has commented that this palynoflora "...is certainly older than the latest Devonian *Retispora lepidophyta* Assemblage and could even be pre-Late Devonian ... (and) datable within the interval mid-Givetian to Frasnian. Biostratigraphically significant components include *Apiculatisporites microconus*, *Geminospora lemurata*, *Verruciretusispora magnifica*, and *Archaeozonotriletes variabilis...*" Thus there may be evidence that the Ningxia *Sinolepis* horizon is somewhat older than the type locality for the genus in the lower Yangtze region.

Biogeography

The distribution of sinolepid antiarchs in apparently non-marine environments in eastern Australia and China but nowhere else is of biogeographic interest, as has been noted by several workers (e.g., Young, 1981, 1984c, 1990a; Long, 1983; Burrett *et al.*, 1990). The fact that *Grenfellaspis* is only known from one locality in eastern Australia could be considered to place doubt on the adequacy of sampling of late Devonian vertebrate faunas for biogeographic purposes. However, as just discussed, other evidence of the vertebrate faunal succession in eastern Australia indicates that the Grenfell fauna is one of the youngest Devonian vertebrate assemblages so far known from the area, so the absence of *Grenfellaspis* itself from other faunas is assumed to be due to an age difference. It seems reasonable to infer from their earlier history in South China that sinolepids only dispersed to Australia in the latest Devonian. Many aspects of the Early Devonian fish faunas of the two regions indicate little communication between non-marine faunas, although there is some evidence of shallow marine similarity (e.g., *Buchanosteus* in eastern Australia, *Kueichowlepis* in China). Primitive bothriolepid antiarchs in the Middle Devonian of eastern Australia (*Monarolepis*) and South China (*Dianolepis*), and closely related species of *Bothriolepis* in the Givetian-Frasnian of Antarctica, Australia, and China (Young, 1988a), suggest closer biogeographic ties in the late Middle and Late Devonian. From the wide distribution of *Bothriolepis* (cosmopolitan in the Late Devonian) it seems clear that its range enlargement resulted from a greater capacity to cross

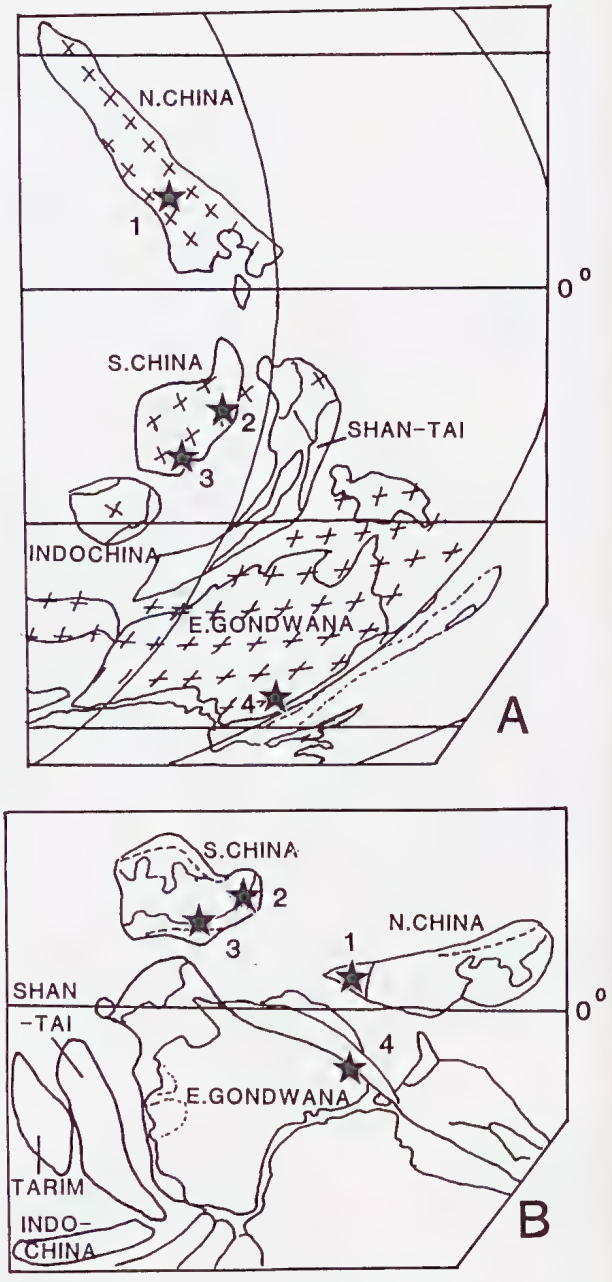

Fig.35. Suggested palaeogeographic relationships between North and South China and East Gondwana in the Late Devonian, showing the four main areas for sinolepid antiarchs (*cf.* Fig.1). 1 - Ningxia Province, North China block (*Sinolepis*); 2 - Nanjing region (*Sinolepis*); 3 - Yunnan-Guangxi region and north Vietnam, South China block (*Xichonolepis*, *Dayaoshania* etc.); 4 - Grenfell region, Tasman Fold Belt, East Gondwana (*Grenfellaspis*). A - after Scotese 1986; B - after Burrett *et al.* (1990).

marine barriers than some other placoderm groups, such as sinolepids or phyllolepids. The complete absence of phyllolepid placoderms from the Devonian of China has been taken to indicate persistent (probably marine) barriers between it and east Gondwana, but as noted in the previous section the Grenfell fauna appears to be younger than the upper biostratigraphic range of phyllolepids in eastern Australia. Thus it may be postulated that the palaeogeographic changes which permitted sinolepids to disperse into east Gondwana were events which postdated the extinction of the Phyllolepida.

Various palaeogeographic reconstructions have been proposed for the Palaeozoic configuration of the tectonic units of east Asia. Figure 35 shows two recent proposals. The maps of Scotese (1986) show the North China block with a similar orientation but much closer to the north-western margin of Australia in the Early Devonian, with an oceanic barrier of increasing width separating North China from South China and Australia in the Late Devonian. This shows no consistency with the biogeographic evidence of sinolepid distribution. Burrett *et al.* (1990) show a northward excursion of east Gondwana towards the palaeoequator, and of North China away from the palaeoequator to 30° north, during

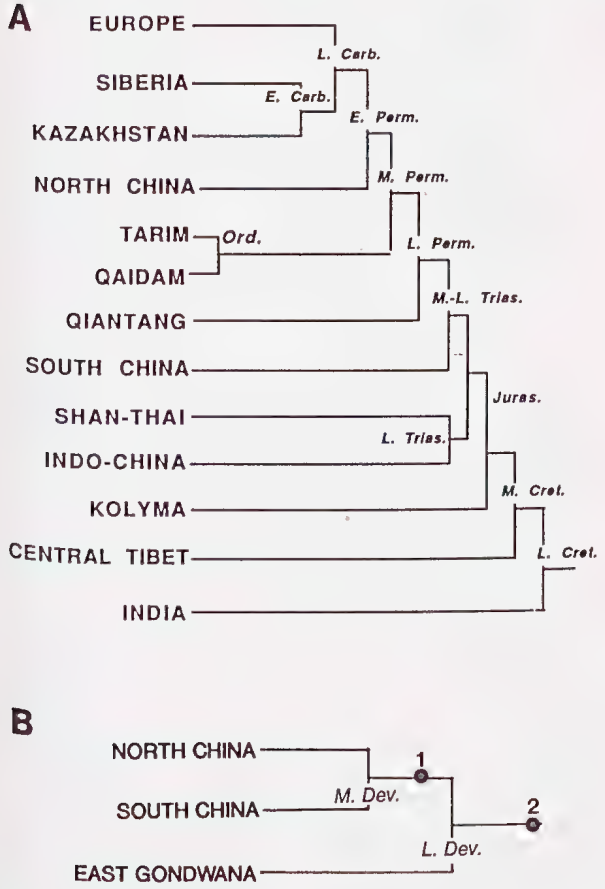

Fig.36. A - accretionary sequence for Asian terranes (after Talent *et al.*, 1987); B - accretionary sequence for three regions based on the following faunal evidence. 1 - occurrence of Givetian quasipetalichthyids and Late Devonian galeaspids and sinolepids in Ningxia; 2 - occurrence of Late Devonian sinolepids in Australia.

the Early - Middle Devonian interval. North China returns to an equatorial position in the Late Devonian to lie adjacent to Australia and South China (Fig.35B). This reconstruction was proposed to take account of the sinolepid evidence, and the occurrence of a similar Late Devonian flora in Ningxia and South China, but as noted above there may be palynological evidence that the Zhongning Formation is older (?Frasnian) than the Wutung and Sanmentan Formations of South China. This is consistent with an earlier faunal exchange of *Remigolepis* between China and Australia - this genus is known from older deposits in eastern Australia than the *Grenfellaspis* assemblage, possibly as old as Frasnian, and undescribed *Remigolepis* species from the Hervey Group of central NSW (generally regarded as early Famennian in age) include very similar and presumably closely related species to those described by Pan *et al.* (1987) from Ningxia (Zhang Guorui, personal observation). In contrast the sinolepids are generically distinct between China and Australia.

The palaeogeographic history of the areas under consideration here may also be represented as area cladograms. Talent *et al.* (1987) present an accretionary sequence for Asian terranes which in South China and North China come together in the Triassic (Fig.36A). A Mesozoic closure has been accepted in the literature for some time (e.g., Burrett, 1974; McElhinny *et al.*, 1981), but the vertebrate evidence discussed here strongly indicates coalescence by the late Middle Devonian (Fig.36B). Resolution of this inconsistency is complicated by the fact that the Zhongning Basin of Ningxia (Pan *et al.*, 1987, figs 2,9) may have had a separate Palaeozoic history (the Hexizoulang Terrane of Li *et al.*, 1985), detaching from South China sometime after the Devonian (Burrett *et al.*, 1990). If correct then the sinolepid biogeographic evidence has no bearing on the palaeogeographic history of the North China terrane. Wang (1985: 141) shows the area of the Zhongning Basin to lie on the south-east margin of their geotectonic unit IIB3 (Alxa Massif), at the edge of the North Qilian fold zone (IIG1), but make no suggestions as to its separate palaeogeographic history in relation to the North China block.

A second complicating factor is the suggestion (Hsu *et al.*, 1988) that the South China fold belt may have been a separate terrane which did not coalesce with the Yangtze block until Mesozoic time. The sinolepid and other evidence (similar vertebrate, macroplant and miospore assemblages in the Sanmentan and Wutung Formations on either side of the proposed suture) is completely inconsistent with this hypothesis.

To conclude, some other faunal evidence consistent with the sinolepid distribution pattern may be briefly summarised. In the latest Devonian-Early Carboniferous close affinity between Australia and China is also indicated by freshwater leaiid ostracods, which are known in the Devonian only from China, but appear in the Early Carboniferous of north-western (Anderson Formation) and north-eastern (Drummond Basin) Australia, and only become widespread later in the Carboniferous,

in Namurian and younger strata (P.J. Jones, personal communication). Some groups of Early Carboniferous brachiopods show a similar pattern (K.S.W. Campbell, personal communication; the sister taxa *Eochoristes* and *Ectochoristes*; see Chu, 1933; Campbell, 1957). A conodont species from the Bonaparte Basin of north-western Australia, originally described as *Polylophodonta* sp. A, which has a restricted range within the late Famennian Buttons Beds (Jones, 1985, fig.2), is probably conspecific (P.J. Jones, personal communication) with *Rhodalepis polylophodontiformes* of Wang & Yin (1985), only known from the Xiakou section of the Rongxian Formation, in Guangxi Province (lower-middle *praesulcata* Zone). Other examples showing a similar pattern are likely to be forthcoming, since this preliminary evidence suggests that both non-marine and shallow marine organisms were controlled by similar biogeographic factors.

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APPENDIX I

Abbreviations:- L.ad - length of anterior division; L.pd - length of posterior division; L.am - length of anterior margin; L.pm - length of posterior margin.

Table 1. Measurements and ratios of the AMD of *Grenfellaspis* (unit : mm)

spec.no.	Length (L)	Breadth (B)	B/L	L.ad	L.pd	L.ad / L.pd	L.am	L.pm
AMF 56328	59	28	47	45	14	3.2	16	13
AMF 61447	50	30	60	39	10	3.9	13	15
AMF 78684	51	30	59	40	11	3.6	14	14
AMF 78695	47	23	49	–	–	–	15	–
CPC 29110	37	23	62	27	10	2.7	11	12

Table 2. Measurements and ratios of the PMD of *Grenfellaspis* (unit : mm)

spec.no.	L	B	B/L	L.am	L.pm
AMF 56136a	54	25	46	16	22
AMF 56136b	43	23	54	11	19
AMF 56175	53	24	45	18	14
AMF 56282a	31	17	55	11	16
AMF 56282b	33	15	45	–	–
AMF 56294b	43	21	49	15	17
AMF 56324	31	23	74	15	19
AMF 56328a	49	22	45	–	21
AMF 56328b	41	19	46	10	15
AMF 56362	50	22	44	–	–
AMF 56364	40	22	55	14	19
AMF 79202	48	33	69	24	21
AMF 79203	38	25	66	17	21

Table 3. Measurements of AMD of *Dayaoshania* (unit : mm)

spec.no	L#	B	B/L	L.ad	L.pd	L.ad / L.pd	L.am	L.pm
MGV 1947	30	15	50	22	8	2.8	5	9
MGV 1950	24	11	46	20	6	3.3	–	5
IVF 2	30	17	57	24	5	4.8	5	11
IVF 4	27	15	56	22	5	4.4	5	10
IVF 5	30	15	50	24	8	3.0	6	10

external measurement excluding posterior *oa*

Table 4. Measurements of PMD of *Dayaoshania* (unit : mm)

spec.no	L	B	B/L	L.am	L.pm
MGV 1947	26	17	65	8	18
IVF 2	26	16	62	11	–
IVF 4	26	18	69	–	17

Table 5. Measurements of AMD of *Xichonolepis* (unit : mm)

spec.no	L.	B.	B/L	L.ad	L.pd	L.ad / L.pd	L.am	L.pm
V 2965.3	98	80	82	68	30	2.3	–	28
V 5076	115	85	74	87	28	3.1	–	43
V 5077	103	90	87	85	25	3.4	14	43
V 9057.8	66	49	74	51	15	3.4	10	26
V 9058	41	20	49	31	11	2.8	6	16

Table 6. Data matrix for 11 characters used in constructing the cladograms of Figure 34. Character polarity is discussed in the text. For list of characters see caption to Figure 34. (0 = primitive character state; 1 = derived character state; – = character state unknown).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
ASTEROLEPIDOIDS	1	0	0	0	0	1	1	1	1	1	1
BOTHRIOLEPIDOIDS	0	1	0	0	0	1	1	1	1	1	1
Sinolepis	1	1	1	1	1	–	0	0	–	1	–
Grenfellaspis	1	1	1	1	1	0	0	0	0	1	1
Xichonolepis	0	0	0	0	1	–	–	–	–	1	1
Dayaoshania	0	0	0	0	1	–	–	–	–	1	–
Procondylolepis	–	–	–	–	–	0	0	0	0	0	0
YUNNANOLEPIDS	0	0	0	0	0	–	–	–	0	–	0

APPENDIX II

Abbreviations used in text and figures

ADL	anterior dorsolateral plate
AMD	anterior median dorsal plate
AVL	anterior ventrolateral plate
ac	anterior corner of PNu
al	anterolateral corner of Nu
ar3d	external articular area of Cd1
ar2v	internal articular area of Cv1
ar3v	external articular area of Cv1
art.d	dorsal articular area
art.v	ventral articular area
a.un	unornamented area beneath fossa articularis pectoralis
Cd1-5	dorsal central plates 1-5 of pectoral fin
Cv1-5	ventral central plates 1-5 of pectoral fin
c4	corner between middle and posterior divisions of mesial margin of ventral lamina of AVL
c5	posteroventral corner of AVL
c.al	anterolateral corner of subcephalic division of ventral lamina of AVL
c.am	anteromesial corner on anterior margin of ventral lamina of AVL
c.Cv2	margin in contact with Cv2 plate
c.Ml2	margin in contact with Ml2 plate
c.Mm1,2	margin in contact with Mm1 or Mm2 plates
c.rc	rostro-caudal canal
cf.ADL	area overlapping ADL
cf.PVL	area overlapping PVL
cit	crista transversalis interna anterior
cit 1,2	anterior and posterior divisions of cit
cl	anterolateral corner of PNu
co.v	ventral thickening of brachial condyle
cr.dm	dorsomesial ridge of pectoral fin
cr.tv	transverse nuchal crista of head
dc	dorsal corner of lateral lamina of AVL and PVL
d.end	opening of canal for endolymphatic duct
dlr	dorsolateral ridge of trunk-armour
f.ax	foramen axillare of AVL
fm	unpaired insertion fossae on head-shield for levator muscles
fp	funnel pit of processus brachialis
gr	groove
grm	ventral median groove on dorsal wall of trunk armour
ifc	infraorbital sensory line on head-shield
L	lateral plate
lcg	main lateral line sensory groove
Ml2-5	lateral marginal plates 2-5 of pectoral fin
Mm1	mesial marginal plate 1
Mm2	mesial marginal plate 2
MV	median ventral plate
MxL	mixilateral plate
m1-3	anterior, middle and posterior divisions of mesial margin of AVL plate
mc	lateral corner of Nu
mp	middle pit-line groove
Nu	nuchal plate
nm	obtected nuchal area of headshield
nPP	postpineal notch of Nu
nprl	prelateral notch of head-shield
oa.ADL	area overlapped by ADL
oa.AVL	area overlapped by AVL
om	orbital margin
orb	orbit
PM	postmarginal plate
PMD	posterior median dorsal plate
PNu	paranuchal plate
PP	postpineal plate
PrL	prelateral plate
PrM	premedian plate
PVL	posterior ventrolateral plate
pbr	processus brachialis
pc	posterolateral corner of Nu
prc	prepectoral corner
pr.dep	preorbital depression
prdm	dorsomesial process
pt1	anterior ventral pit of dorsal wall of trunk armour
ptoc	postobstantic corner
r.dm	dorsomesial ridge on Cv1
r.sg	ridge along inner edge of sensory groove
ri	ridge
Sm	semilunar plate
sap	lateral subanal process of PVL plate
sg	sensory groove
soa	subobstantic area
soc	anterior section of supraorbital sensory line on PrM
sop	supraoccipital pit of head-shield
T	terminal plate

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Two New Dorippid Crabs from Australia (Crustacea: Decapoda: Dorippidae)

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ABSTRACT. Two new species of *Dorippe* are named, *D. glabra* from Chambers Bay, Northern Territory and *D. trilobata* from the Admiralty Gulf, Western Australia. A key to Australian species of *Dorippe* is presented.

MANNING, R.B., 1993. Two new dorippid crabs from Australia (Crustacea: Decapoda: Dorippidae). Records of the Australian Museum 45(1): 1–4.

The two species of *Dorippe* named here were found among the collection of Dorippinae in the Australian Museum, Sydney. Now seven species of *Dorippe* are known from the Indo-West Pacific region; five species were recognised by Holthuis & Manning (1990) in their revision of the Dorippinae from that region. Only one species of *Dorippe*, *D. quadridens* (Fabricius, 1793), previously had been recorded from Australia.

Both holotypes are in the collections of the Australian Museum, Sydney (AM).

Systematic Account

Dorippe glabra n.sp.

Fig.1

Material. HOLOTYPE, ovigerous female, AM P13363, Chambers Bay, NT, Australia, 12°13'S 131°35'E, Otter trawl, 38 m, A.A. Racek, 7 Nov. 1959.

Diagnosis. Anterolateral margins of carapace, anterior to epibranchial region, smooth, unarmed. Lower orbital margin with 3 spines arranged in row. Carpus of cheliped granular. Merus and carpus of second and third pereopods naked, flattened. Merus of third pereopod 5 times as long as high.

Description. Carapace distinctly sculptured, grooves well marked but shallow, larger tubercles distinct, surface of tubercles granular. Surface of carapace largely smooth and naked, with few scattered short hairs, especially laterally, not obscuring surface ornamentation. Protogastric tubercles each with 4 granules. Mesogastric tubercle bilobed, surface with granules. Urogastric tubercle small, granular. One tubercle on mesial end of ridge anterior to branchial groove. Branchial lobes not markedly swollen, smooth. Lateral branchial tubercle large but smaller than dorsal branchial tubercle, latter largest of all tubercles on carapace. Branchial region also with smaller tubercles posterolateral to dorsal branchial tubercle, connected to it by low carina. Median ridge of cardiac region Y-shaped; posterior tubercle of cardiac region conical,

lateral tubercles low, broad, dimpled. Anterolateral margin of carapace smooth, unarmed anterior to epibranchial region, there with low tubercles.

Frontal teeth low, bluntly triangular, apices broadly rounded, median incision U-shaped. Frontal teeth wider than inner orbital teeth, latter low, apices rounded, extending to base of median incision of front; 1 pair of low postfrontal prominences present. No spinules or granules present on anterior margin of front or on dorsal orbital margin.

Lower orbital margin with row of 3 blunt spines on outer margin of inner orbital tooth, margin with 1 low tubercle below posteriormost spine.

Chela of female (male unknown) with palm higher than long; outer surface of palm almost entirely naked and smooth, some granules visible basally under magnification. Carpus covered with granules, sparsely hairy.

Merus of second pereopod 4 times as long as high, merus of third pereopod 5 times as long as high. Segments of walking legs naked, largely smooth, dorsal ridge of carpus finely granular. Propodus of second pereopod about 3.5 times as long as high, of third pereopod 4 times as long as high. Dactylus slender, curved, longer than propodus on both legs.

Sternites of first and second legs with granular transverse carinae, interrupted on midline.

Female abdomen with teeth of third and fourth somites rather sharp, median larger and blunter than remainder. Fifth somite lacking indication of median tooth on tuberculated transverse ridge. Gonopore as illustrated.

Size. Unique ovigerous female holotype, carapace length 24.3 mm, carapace width 26.7 mm.

Remarks. This new species can readily be distinguished from the five species of *Dorippe* recognised by Holthuis & Manning (1990). It differs from *D. frascone* (Herbst, 1785) in having granules on the carpus of the cheliped and in having the transverse ridge on the fourth abdominal somite much rougher.

From *D. irrorata* Manning & Holthuis, 1986 it can be distinguished by the smooth palm of the chela, the presence of only three teeth on the lower orbital margin, and in having the anterolateral margin of the carapace unarmed anterior to the epibranchial region. It can be distinguished from *D. quadridens* (Fabricius, 1793) by the naked meri of the second and third pereopods which in *D. quadridens* are setose, often densely so. It differs from *D. sinica* Chen, 1980 in having the meri of the second and third pereopods flattened rather than almost cylindrical and naked rather than hairy and in having

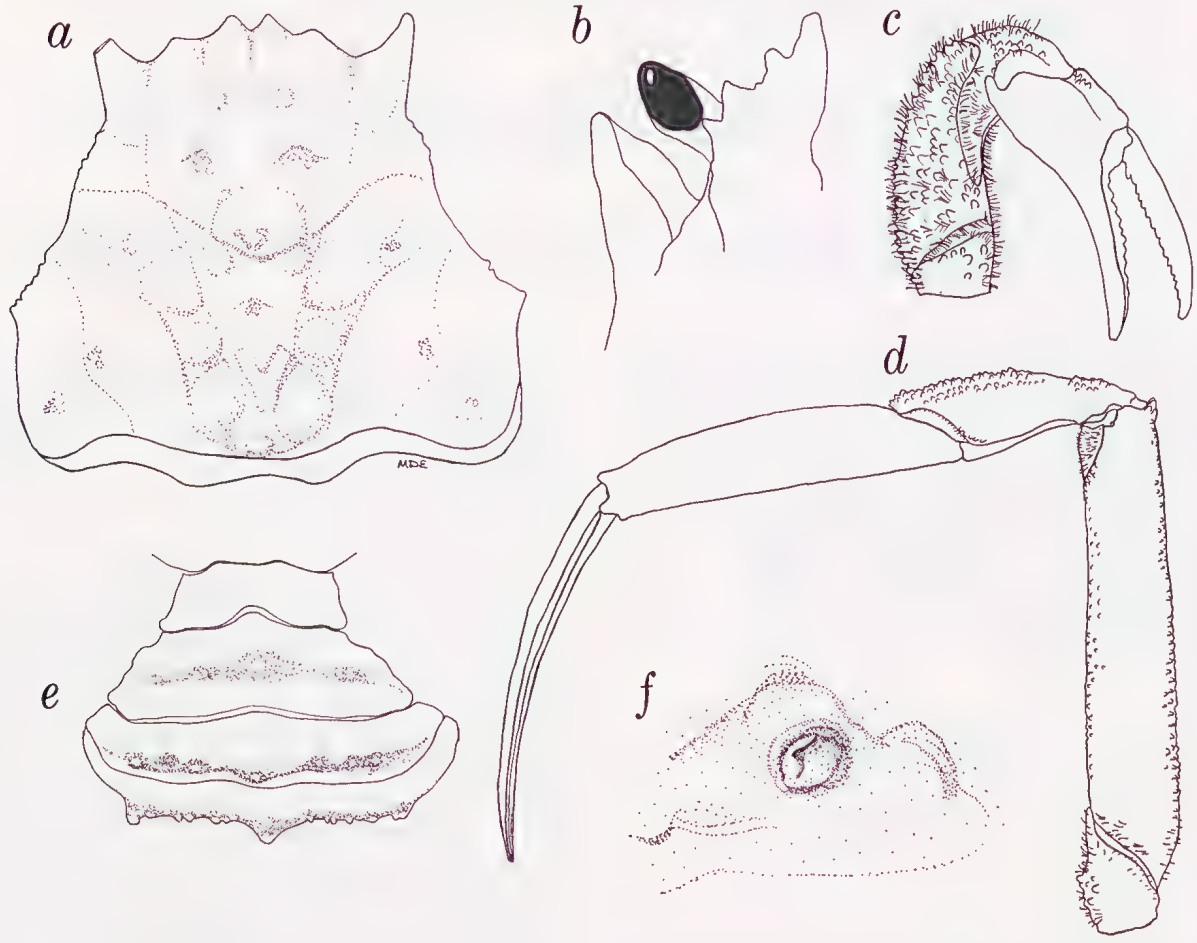

Fig.1. *Dorippe glabra* n.sp., ovigerous female holotype, carapace length 24.3 mm: a, carapace; b, orbit, ventral view; c, cheliped; d, third pereopod; e, abdomen, ventral view; f, gonopore.

the dorsal sculpture of the carapace much less pronounced, with the dorsal tubercles lower. Its short second and third pereopods distinguish it from both *D. tenuipes* Chen, 1980, and the long-legged species described below, *D. trilobata*.

The unique holotype of *D. glabra* was part of a large collection identified as *D. quadridens*. It could be distinguished on sight from all of the other specimens in that lot by the naked meri of its second and third pereopods.

Etymology. The specific name is from the Latin, *glabra*, bare.

Dorippe trilobata n.sp.

Fig.2

Material. HOLOTYPE, male, AM P27124, off Mitchell River, Admiralty Gulf, Western Australia, 13°52'S 126°45'E, Otter trawl over silty bottom, 18 m, C. O'Connor, 18 Apr. 1978.

Diagnosis. Anterolateral margins of carapace, anterior to epibranchial region, smooth, unarmed. Lower orbital margin with 3 teeth arranged in row. Carpus of cheliped granulate. Merus and carpus of second and third pereopods sparsely setose, flattened. Merus of third pereopod more than 6 times as long as high. Second somite of male abdomen with 3 sharp conical projections.

Description. Carapace appearing naked, grooves deep, larger tubercles low but distinct, latter with sparse setae under magnification. Protogastric, mesogastric and urogastric tubercles low, granular. Of tubercles on ridge anterior to cervical groove, innermost only distinct. Branchial lobes not markedly swollen. Cardiac region with distinct Y-shaped carina, submedian and posterior tubercles low. Lateral branchial tubercle distinct but small, from it line of low granules extending anteriorly;

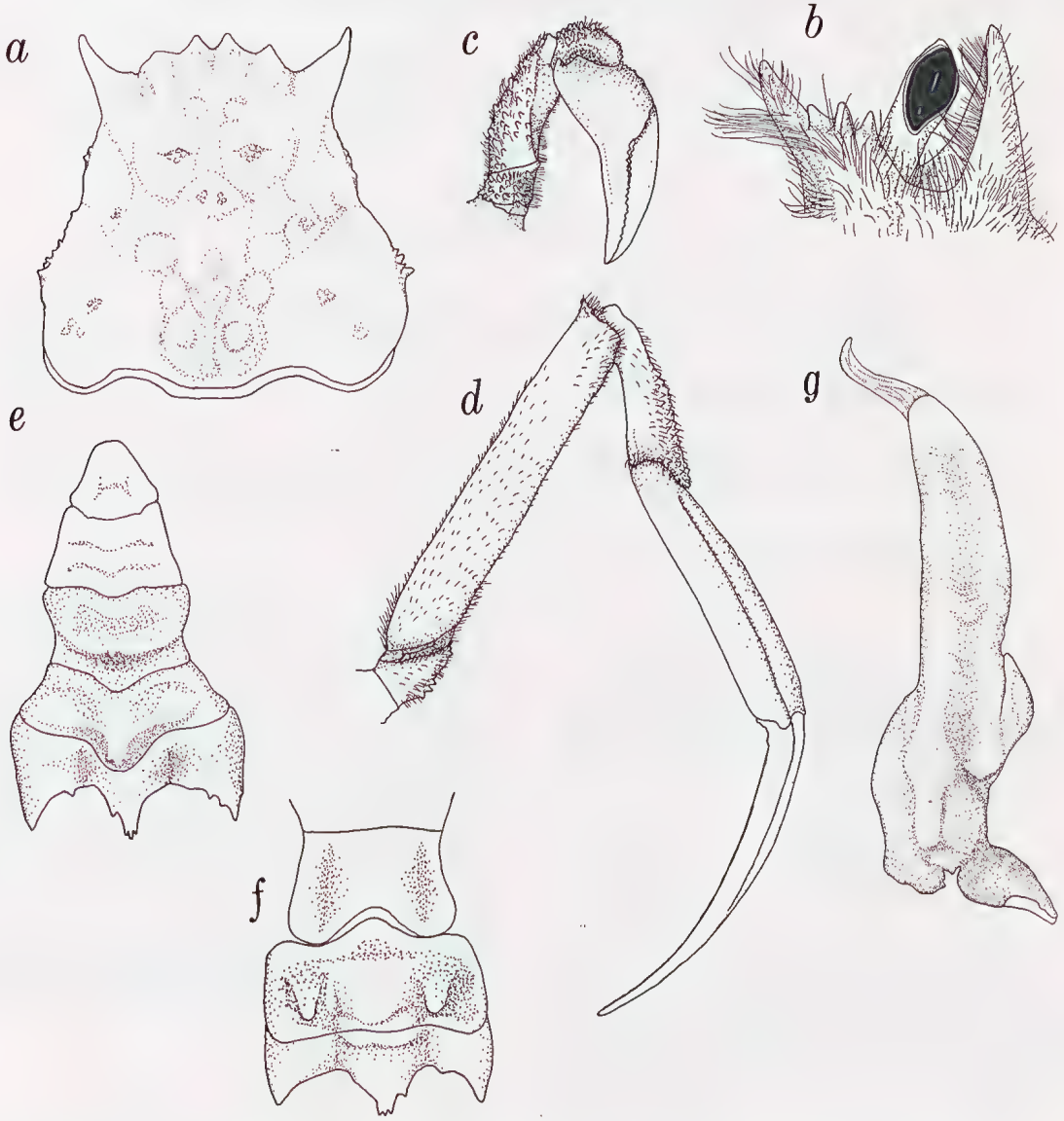

Fig.2. *Dorippe trilobata* n.sp., male holotype, carapace length 20.5 mm: a, carapace; b, orbit, ventral view; c, cheliped; d, third pereopod; e, abdomen, ventral view; f, abdomen, dorsal view; g, gonopod.

mesial dorsal branchial tubercle largest.

Frontal teeth triangular, rounded dorsally. Inner orbital angles wider and shorter than frontal teeth, extending to base of median incision of front. Anterior margin of front and posterior dorsal margin of orbit unarmed. Anterolateral margin of carapace unarmed anterior to epibranchial region, low tubercles present there.

Lower margin of orbit with 3 sharp spines on outer margin of inner suborbital tooth, margin otherwise unarmed.

Chela of male (female unknown) with palm higher than long, outer surface naked and largely smooth, some granules present basally. Carpus with outer surface granular.

Second and third pereopods long and slender. Merus of second pereopod 5.6 times as long as high, merus of third pereopod more than 6 times as long as high; merus of both legs sparsely setose, ornamented with at most few granules. Carpus setose, granular dorsally. Propodus of second pereopod 4 times as long as high, of third pereopod 4.5 times as long as high, naked on both legs. Dactylus longer than propodus on each leg.

Sternites of first 3 pereopods each with transverse carina, interrupted in midline. Second and third somites of male abdomen each with 3 sharp, conical projections, median projection of second somite widest; fourth somite with distinct median spine; fifth somite with 2 low median elevations, anteriormost larger.

Gonopod as illustrated.

Size. Unique male holotype, carapace length 20.5 mm, carapace width 21.1 mm.

Remarks. This new species resembles *D. tenuipes* Chen, 1980 and with that species differs from all other species of *Dorippe* in having elongate second and third pereopods, with the merus of the third pereopod six or more times longer than high. *Dorippe trilobata* differs from *D. tenuipes* in lacking lateral spines on the carapace anterior to the epibranchial region, in having only three spines on the lower margin of the orbit, and having much stronger and sharper conical tubercles on the second and third somites of the male abdomen; *D. tenuipes* lacks the median spine on the fourth abdominal somite. In addition, the second and third pereopods are not as slender and elongate as in *D. tenuipes*.

Etymology. The specific name is from the Latin, *tri-*, three, and *lobatus*, lobed, referring to the three-lobed projection on the second abdominal somite in the male.

Key to Australian Species of *Dorippe*

1. Merus of third pereopod more than 6 times as long as high ..... *D. trilobata* n.sp.

—— Merus of third pereopod about 5 times as long as high 2

2. Meri of second and third pereopods covered with pubescence. Lower orbital margin with 5-6 spines ..... *D. quadridens* (Fabricius, 1793)

—— Meri of second and third pereopods naked. Lower orbital margin with 3 spines ..... *D. glabra* n.sp.

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A New Genus of Macrophthalmine Crab (Crustacea: Decapoda: Ocypodidae) from Eastern Australia

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ABSTRACT. A new genus and species of macrophthalmine is described from eastern Australia. *Enigmaplax* is separable from *Macrophthalmus* by its exceptionally wide front and the pointed not spooned chelae.

DAVIE, P.J.F., 1993. A new genus of macrophthalmine crab (Crustacea: Decapoda: Ocypodidae) from eastern Australia. Records of the Australian Museum 45(1): 5–9.

For some years a small grapsoid crab has been appearing in samples made from various coastal and estuarine localities along the eastern coast of Australia. This species was first reported on from the Brisbane River by Snelling (1959) and tentatively referred to *Cyrtograpsus*. Since then it has been found from numerous localities, and the discovery of a large collection of this species from *Zostera* beds around Pittwater, Sydney, in the Australian Museum, prompted the author to investigate its status. Its rightful place is in the family Ocypodidae where a new genus must be described to accept it.

Abbreviations are as follows: QM – Queensland Museum, AM – Australian Museum. All measurements are of maximum carapace breadth unless otherwise stated. Drawings were made using a camera lucida.

Enigmaplax n.gen.

Type species. *Enigmaplax littoralis* n.sp., by original designation.

Gender. Feminine.

Diagnosis. Carapace flattened, quadrangular, lateral margins subparallel, dentate. Frontal width about 0.4 times fronto-orbital width. Postfrontal lobes sharply defined, straight. Orbits large, lower border complete, no infraorbital crest. Antennules transverse or slightly oblique; inter-antennula septum narrow. Antennae in the orbital hiatus. Central region of epistome distinctly convex. Maxillipeds do not close the buccal cavern; flagellum inserted medially on the anterior margin; merus smaller than ischium; no hairy ridge; exopod narrow. Chelipeds weak, cylindrical, cutting margins evenly serrated, but with basal molariform tooth differentiated in adult males, tips of fingers pointed. Legs slender; dactyls long, curved, unarmed; merus with subdistal tooth on anterior margin; no hairy ridged pouch between bases of first and second walking legs. Abdomen of male of 7 segments; evenly tapering; no medial constrictions.

Enigmaplax littoralis n.sp.

Figs 1a-l, 2a,b

Type material. HOLOTYPE, AM P20789, male (6.0 mm), Careel Bay, Pittwater, Sydney, NSW. Upper *Zostera*, 31 Oct. 1974, P. Hutchings. PARATYPES, QM W15087, 1 male, 2 females (3.0 - 4.0 mm), in front of Redbank Creek, Trinity Inlet, Cairns, north-east Qld, 11 Dec. 1974, R. Timmins. QM W11905, 2 males (4.5, 4.5 mm), Triangular Island, Shoalwater Bay, north-east Qld, Nov. 1982. QM W11906, female (4.5 mm), Triangular Island, Shoalwater Bay, north-east Qld, Nov. 1982. QM W7441, female (2.8 mm), rocky platform at mouth of Pulgul Creek, Urangan, Hervey Bay, south-east Qld, in crevice under rock, 23 July 1975, P. Davie. QM W7442, 2 males, 9 females (3.0 - 5.0 mm), from *Zostera*, south of Urangan Harbour, Hervey Bay, south-east Qld, 23 July 1975, P. Davie. QM W7415, 2 females (3.2, 4.1 mm), East Huth Creek, main channel between Dinner Island and mainland, Moreton Bay, south-east Qld, subtidal *Zostera* using sweep net, 9 June 1976, J. McNalty & P. Shanco. QM W8950, 2 males (3.3, 4.1 mm), between Dinner Island and Mainland, southern Moreton Bay, south-east Qld, sieved, subtidal, *Zostera*, 9 June 1976, P. Shanco. QM W8775, male (3.9 mm), mouth of Brisbane River, along old Bar Cutting, past Bishop Island, south-east Qld, 22 July 1975, L.H. Park. QM W8774, male (3.7 mm), female (3.7 mm), mouth of Brisbane River, past Luggage Point, south-east Qld, 9 Dec. 1976, L.H. Park. AM P20372, 2 males (6.1, 7.5 mm) 1 female (9.0 mm), Careel Bay, Pittwater, NSW, 8 Nov. 1973, P. Hutchings. AM P20370, 2 females (8.4, 6.7 (ovig.) mm) 2 males (4.3, 4.2 mm), Careel Bay, Pittwater, NSW, 8 Nov. 1973, P. Hutchings. AM P20764, 2 males (5.5, 4.5 mm), Careel Bay, Pittwater, NSW, upper *Zostera*, 31 Oct. 1974, P. Hutchings. AM P20366, 1 female (7.7 (ovig.) mm) 1 male (5.7 mm), Careel Bay, Pittwater, NSW, 8 Nov. 1973, P. Hutchings. AM P9211, 2 ovig. females (6.2, 9.4 mm) 1 male (5.6 mm), Cunnamatta Bay, Port Hacking,

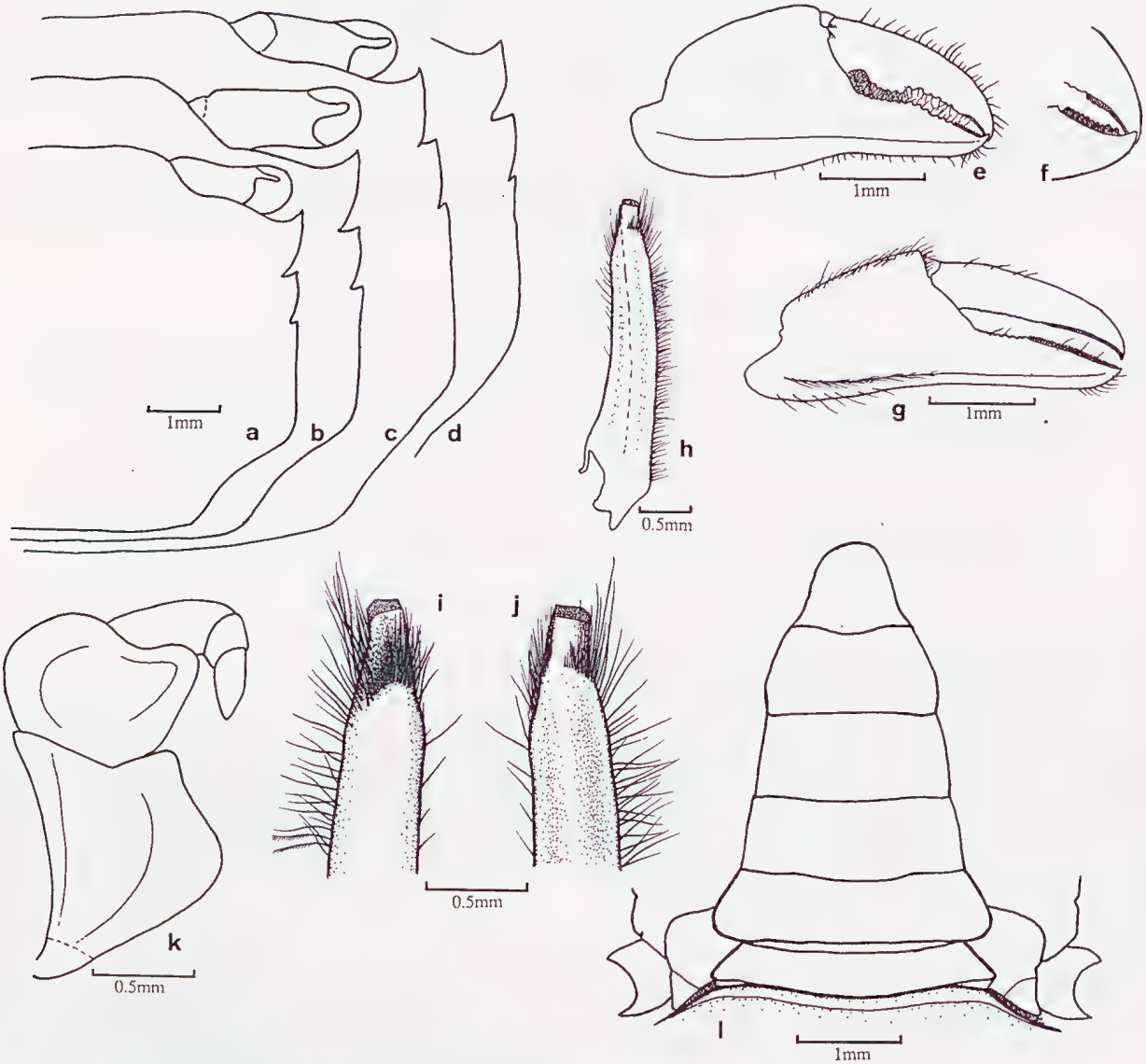

Fig.1. *Enigmaplax littoralis* n.sp., a-d, outline of carapace shapes showing variation in anterolateral borders and degree of frontal lobe development (a = male 6.1 mm, b = male 7.5 mm, c = female 9.0 mm, d = female 9.4 mm); e, right chela of holotype male; f, detail of distal chitinous crests on fingers of holotype male; g, right chela of AM P9211, an ovigerous female; h-j, first male pleopod of AM P20372; k, third maxilliped of holotype; l, abdomen of holotype.

NSW, among weeds on tidal flats at low tide, Oct. 1925, Pres. M. Ward. AM P20364, 1 male (6.7 mm), Riley's Island, Brisbane Waters, NSW, *Zostera*, May 1973, P. Hutchings. AM P20185, 1 female (5.4 mm) 2 males (3.8, 4.2 mm), Towra Point, Botany Bay, NSW, *Zostera*, 1974, P. Ikin. AM P19946, 1 male (4.0 mm), Careel Bay, Pittwater, NSW, 30 July 1973, P. Hutchings. AM P20363, female (ovig.) (7.3 mm), Careel Bay, Pittwater, NSW, lower *Zostera*, 8 Nov. 1973, P. Hutchings. AM P24989, ovig. female (7.3 mm), Careel Bay, Pittwater, Broken Bay, NSW, amongst *Zostera* grass, 16 Feb. 1946, E. Pope. AM P19948, male (3.4 mm), female (4.9 mm), Careel Bay, Pittwater, NSW, 10 June 1973, P. Hutchings. AM P20377, 3 ovig. females (8.6, 6.1, 5.6 mm), Careel Bay, Pittwater, NSW, lower *Zostera*, 8 Nov. 1973, P. Hutchings. AM P19944, ovig. female (8.3 mm), Careel Bay, Pittwater, Sydney, NSW, 30 July 1973, P. Hutchings. AM P19949, female (6.1 mm), Careel Bay, Pittwater, Sydney, NSW, 10 June 1973, P. Hutchings. AM P20373, immat. female (4.9 mm), Careel Bay, Pittwater, Sydney, NSW, *Zostera*, 30 July 1973, P. Hutchings. AM P20787, 2 immat. females (5.3, 5.0 mm), Careel Bay, Pittwater, NSW, *Zostera*, 31 Oct. 1974, P. Hutchings. AM P20766, ovig. female (7.2 mm), Careel Bay, Pittwater, NSW, *Zostera*, 31 Oct. 1974, P. Hutchings.

Description. Carapace: flattened; subquadrate, breadth 1.1 - 1.2 times length; regions slightly defined; distinct gastrocardiac groove; surface smooth or microscopically granular. Lateral borders variable, from subparallel in small specimens to markedly convergent especially in large females, such that point of greatest carapace breadth varies between external orbital angles and posterolateral angles (about level of third walking legs). Three anterolateral teeth; first (external orbital angle) the largest; second of same form but smaller; third the smallest but distinct; sometimes a slight indication of a fourth. Lateral edges more or less minutely granulated; a longitudinal low granulate crest on posterobranchial region near posterolateral carapace margin.

Front prominent; distinctly less than hind width (about 0.7 times); approximately equal to, or even wider than width of orbit; and about 0.42 times fronto-orbital width. Anterior edge in dorsal view usually straight but sometimes may be shallowly bilobed. Upper orbital margin sinuous, slanting towards external orbital angle. Postfrontal lobes sharply defined, straight, separated by

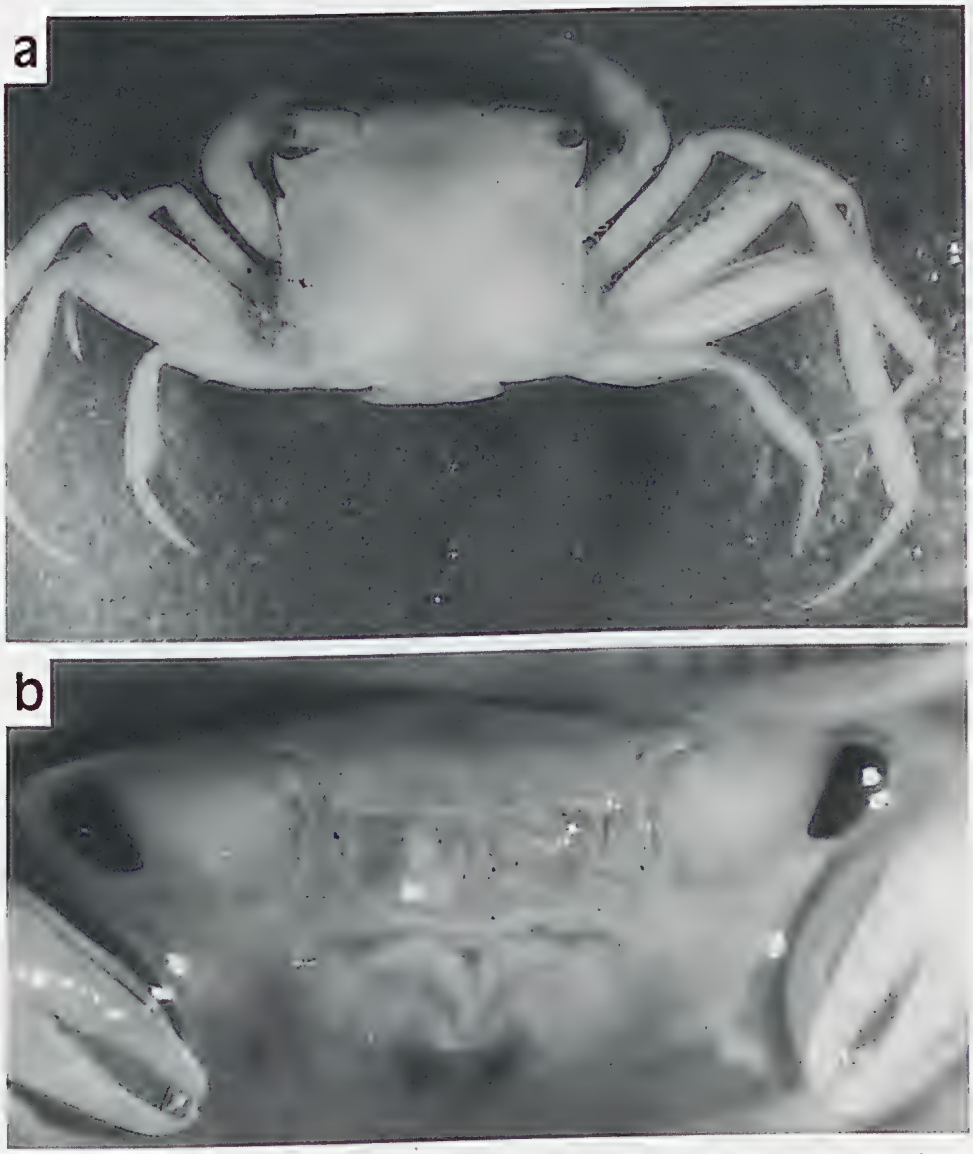

Fig.2. *Enigmaplax littoralis* n.sp., paratype male (QM W7442): a, dorsal aspect; b, frontal view.

narrow notch, and marked by a horizontal line of granules and a row of long feathered setae. Long setae also present along lateral edges of carapace and bases of walking legs.

Eyes large; may reach slightly beyond external orbital angles but usually well short of these, especially in large females. Antennae long reaching almost to tips of corneas; lie within orbital hiatus. A single simple seta arises from tip of penultimate segment of flagellum and varies in length from short to two thirds length of flagellum.

Antennules separated by a narrow septum, basal segment inflated, flagellum lies transversely or slightly obliquely. Epistome quite broad, lower edge sinuous, clearly convex medially. Lower orbital margin entire, finely granular.

Third maxillipeds separated by a median hiatus and do not close buccal cavern; hairy along internal margins. Merus about three quarters length of ischium. Anterior edge of ischium slants down towards upwardly directed lobe of inner anterior margin. External margin of merus rounded; anterior margin concave with carpus emerging more or less centrally. Exopod narrow (length about 5.5 times breadth); width of exopod about 0.4 times width of ischium.

Abdomen does not occupy entire space between hind walking legs; composed of 7 free segments; third segment expanded and forms greatest breadth; other segments taper gradually. Telson breadth 1.4 times length; breadth of penultimate segment 2.5 times length. Telson 1.3 times length of penultimate; breadth of penultimate 1.4 times breadth of telson at base. Telson the longest; segments 4 and 6 subequal; segment 5 slightly longer than 4 and 6. Telson rounded anteriorly.

Chelipeds subequal. Merus with patch of setae on internal face, thickest distally; setae continue onto internal edge of carpus and form a thick mat on inside of palm and fixed finger, extending around gape and along inner margins of both fingers. Merus and carpus unarmed. Palm not especially robust. Length of moveable finger 0.5 - 0.6 times length of palm in males. Fingers pointed distally, cutting margins of both fingers evenly serrated over most of their length, but with distal quarter having chitinous crests; on immovable finger this crest is pectinate, while on dactyl it is a continuous sharp crest. Males sometimes with a more or less distinct differentiated tooth near base of moveable finger. A granulated ridge arises on tip of fixed finger and runs the length of the palm. Lower margin of palm and fixed finger shallowly concave. Moveable finger slightly curved.

Female chelae smaller and more slender than males, without patches of setae on inside of merus, carpus and palm, and with distal chitinous crests on cutting margins of fingers extending back about a half to two thirds of distance towards articulation.

Walking legs: (ratios apply to third walking leg); long (about 2 times carapace width), and slender with length of merus about 3.5 times width. Merus with sharp spine subdistally on anterior margin. Dactylus long, equal in length to propodus, unarmed. Length of merus and basis equal to length of carpus and propodus. Margins of meri of first 3 pairs are slightly convex, but of last pair are straight and parallel. Row of fine long setae on posterior margin of propodus of fourth leg and on posterior and anterior margins of dactylus.

First male pleopod as figured.

Habitat. Intertidal or very shallow subtidal, in *Zostera* beds, algal mats, and under rocks. Snelling (1959) recorded it from the Brisbane River from under stones in the littoral zone from the mouth to about 10 km upstream where salinity would fluctuate from about 15-30 parts per thousand.

Distribution. Eastern Australia from Cairns in the north to Sydney in the south.

Discussion. Snelling (1959) recorded a species from the Brisbane River which she tentatively referred to *Cyrtograpsus*. She wrote to M.W.F. Tweedie of the, then, Raffles Museum in Singapore for confirmation of identification and the following reply was received: 'The series contains two species. One is, I think, conspecific with *Camptandrium paludicola* Rathbun...The other seems to be a species of the same genus... probably undescribed. However, the genus to which these both belong is not, I am almost certain, *Camptandrium*'. Barnard (1955) erected a new genus, *Ilyograpsus*, to receive his *I. rhizophorae*. This species proved to be a junior synonym of *C. paludicola* but the genus *Ilyograpsus* remained valid and so *C. paludicola* was transfered from the Ocypodidae to the Grapsidae.

The other species from Snelling's collections referred to by Tweedie would seem to be *Enigmaplax littoralis* as this species does bear certain resemblances to *Ilyograpsus paludicola* and during extensive collecting in the Brisbane River and from other south-eastern Queensland localities no other species has been found which could be considered a close ally. *Shenius anomalum* (Shen, 1935) is also of similar appearance to *I. paludicola* but has not yet been reported from Australia. According to Serène (1974) it belongs in the Dotillinae (= Scopimerinae). The strong medial constriction of the male abdomen and the shape of the first male pleopod in *S. anomalum* both indicate that there is no close affinity with *Enigmaplax*.

Enigmaplax is difficult to place into either the Ocypodidae or the Grapsidae because of the overlap in the familial definitions. It does, for example, look far closer to species of *Hemigrapsus* and *Euchirograpsus* than to any of the ocypodids. Within the Grapsidae, however, only members of the subfamilies Varuninae and Sesarminae have the male abdomen not covering the surface of the sternum between the last pair of ambulatory legs. It must be excluded from the Varuninae because the lower orbital border is complete and not supplemented by a lower orbital crest, and the Sesarminae is not suitable as there is no hairy ridge on the third maxillipeds.

Of the subfamilies of the Ocypodidae, the Macrophthalminae alone is suitable. Sakai (1976: 598)

defines this subfamily as follows: 'Carapace broadly quadrilateral and flattish. Eyestalks often remarkably long; antennules folded transversely and their flagellum developed; inter antennular septum very narrow. External maxillipeds leave a more or less wide median hiatus; no hairy-ridged pouch between bases of first and second ambulatory legs'. *Enigmaplax littoralis* agrees well with this definition and therefore it is placed here. The front is exceptionally wide when compared with other species within the Macrophthalminae although *Australoplax tridentata* does represent a comparatively wide condition. Barnes (1967, 1968) postulates that predation has been the major factor influencing the evolution of long ocular peduncles (and consequent narrowing of the front). *Enigmaplax littoralis* being of small size, cryptic colouration, and living in littoral or shallow sublittoral habitats which provide good concealment (e.g., algal matts, *Zostera* beds, under stones) would suffer little from 'terrestrial' predators and consequently there would be no selective advantage in particular elongation of the eyestalks.

Enigmaplax littoralis agrees on most points with the hypothesised ancestral *Macrophthalmus* of Barnes (1967). The main points of departure are that the merus of the external maxilliped is smaller than the ischium as opposed to subequal; and the epistome has a distinctly convex central region, not straight. It cannot be placed in the genus *Macrophthalmus* because of the relatively much broader front, and the pointed, non-spooned fingers of the chelae. Nevertheless it agrees with *Macrophthalmus* in many ways including the presence of a differentiated molariform tooth on the cutting margin of the dactyl and in the general form of the first male pleopod. Species of the subgenus *Mopsocarcinus* approach *Enigmaplax* in their quadrate carapace and broader front but even so the frontal width is still considerably narrower - *M. boscii* has a frontal width of about 0.25 times fronto-orbital width; *M. punctulatus*, about 0.29 times; *Enigmaplax littoralis*, about 0.42 times. Also those two species differ significantly in the fact that the merus and ischium of the third maxillipeds are subequal. *Macrophthalmus* (*Hemiplax*) *hirtipes* also has a very wide front without a medial constriction, but the carapace is much broader than long, and the eyestalks are longer and comparatively slender.

The only other genus recognised within the Macrophthalminae, *Australoplax*, differs in the shape of the carapace, which is stout and relatively deep; the chelae, which do not have differentiated teeth on the cutting margins, and have an external mat of hair in the gape; and by the remarkable shape of the male abdomen.

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Deep Sea Crabs of the Tasman Seamounts (Crustacea: Decapoda: Brachyura)

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Abstract. This study of a collection of deep sea crabs from the Tasman Sea contains eleven species, of which five are new: *Halicarcinus lucasi, Macropodia trigonus, Leptomithrax depressus, Kimbla franklini, Pugettia tasmanensis.*

Richer de Forges, B., 1993. Deep sea crabs of the Tasman seamounts (Crustacea: Decapoda: Brachyura). Records of the Australian Museum 45(1): 11–24.

The collection of crabs in this study come from an Australian Museum cruise in May 1989 on board the RV *Franklin*, a CSIRO vessel. Part of the material from the cruise has already been the object of publications with the description of new material, *Sphenocarcinus lowryi* Richer de Forges, 1992, and a new genus (in press).

The zone explored is situated in the north-western Tasman Sea, the southern Coral Sea, and along the east coast of Australia. Most of the dredging, using an epibenthic sledge, took place in the upper bathyal zone, between 1600 and 120 m. One of the objectives of this exploratory cruise was the sampling of the guyots aligned from north to south between 21°S (Chesterfield Islands) and 38°S. These guyots came from a volcanic hot spot, and are evidence of the movement towards the north of the Indo-Australian plate (Van der Linden, 1969, 1970; Slater & Goodwin, 1973); the oldest date from 28 M.Y. (Oligocene). Their small size and the huge oceanic distances which separate them make these guyots into oases of bathyal fauna in the middle of an immense desert of abyssal depths.

The small collection studied here contains eleven species, each represented by a small number of specimens. Five new species are described. The great originality of this fauna shows that the sampling of the bathyal zone is far from satisfactory.

All material is lodged in the Australian Museum, Sydney (AM) or the New Zealand Oceanographic Institute, Wellington (NZOI).

Species List

Homolidae
Latreillopsis aff. *multispinosa* Ihle, 1912
Hymenosomatidae
Halicarcinus lucasi n.sp.
Majidae
Achaeus curvirostris (A. Milne Edwards, 1873)
Achaeus sp.
Macropodia trigonus n.sp.
Leptomithrax tuberculatus Whitelegge, 1900

Leptomithrax depressus n.sp.
Thacanophrys sp.
Kimbla franklini n.sp.
Pugettia tasmanensis n.sp.

Geryonidae

Chaceon bicolor Manning & Holthuis, 1989

Systematic Account

Homolidae White, 1847

Latreillopsis Henderson, 1888

Latreillopsis **aff.** *multispinosa* Ihle

Fig.1a,b

? *Latreillopsis multispinosa* Ihle, 1912: 211.–Ihle, 1913: 52, pl.4, figs 19-21.
Latreillopsis aff. *multispinosa*.–Guinot & Richer de Forges, 1981: 556, figs 4G, 6B, pl.VII, 2.

Material examined. 1 ovigerous female, 29 x 28.4 mm, AM P39432, Britannia Guyot, Tasman Sea, 28°18.48'S 155°38.62'E, beam trawl, 415 m, 10 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 48.

Remarks. This large female specimen presents, with the *Latreillopsis multispinosa* from the Kai Islands, the same differences noted in the material from New Caledonia (Guinot & Richer de Forges, 1981: 556): the merus of pereiopod 4 is armed with three strong spines; the gastric zone carries five long spines and two spinules; and the basis-ischium of pereiopod 4 carries two strong spinules.

This specimen is the only Homolidae collected during the 49 dredgings of this cruise. Other members of this family are known from the Australian coasts. Davie & Short (1989) have recorded: *Latreillopsis bispinosa, L. petterdi, Paromola japonica, Paromolopsis boasi, Homola orientalis, Homolochunia kullar.*

Hymenosomatidae Macleay, 1838

Halicarcinus White, 1846

Halicarcinus lucasi **n.sp.**

Fig.2a,b

Material examined. HOLOTYPE, female, ovigerous, 2.2 x 2 mm, AM P39429, Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, 244 m, 2 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 8.

Etymology. This species is dedicated to Dr J.S. Lucas who did the most comprehensive work on this family.

Description. Very small species, the adult female only measures 2 mm in width. Flat, circular carapace, slightly depressed, edged with a light rim and with grooves defining the areas.

The rostrum is long and thin, shaped with a single tip slightly curved towards the top at its end, a few bristles on the edges; the rostrum is separated from the rest of the carapace by the rim which surrounds it. Anterolateral edge slightly concave; anterolateral angle not well marked, does not form a tooth; posterolateral and posterior edge make a continuous curve, perfectly circular.

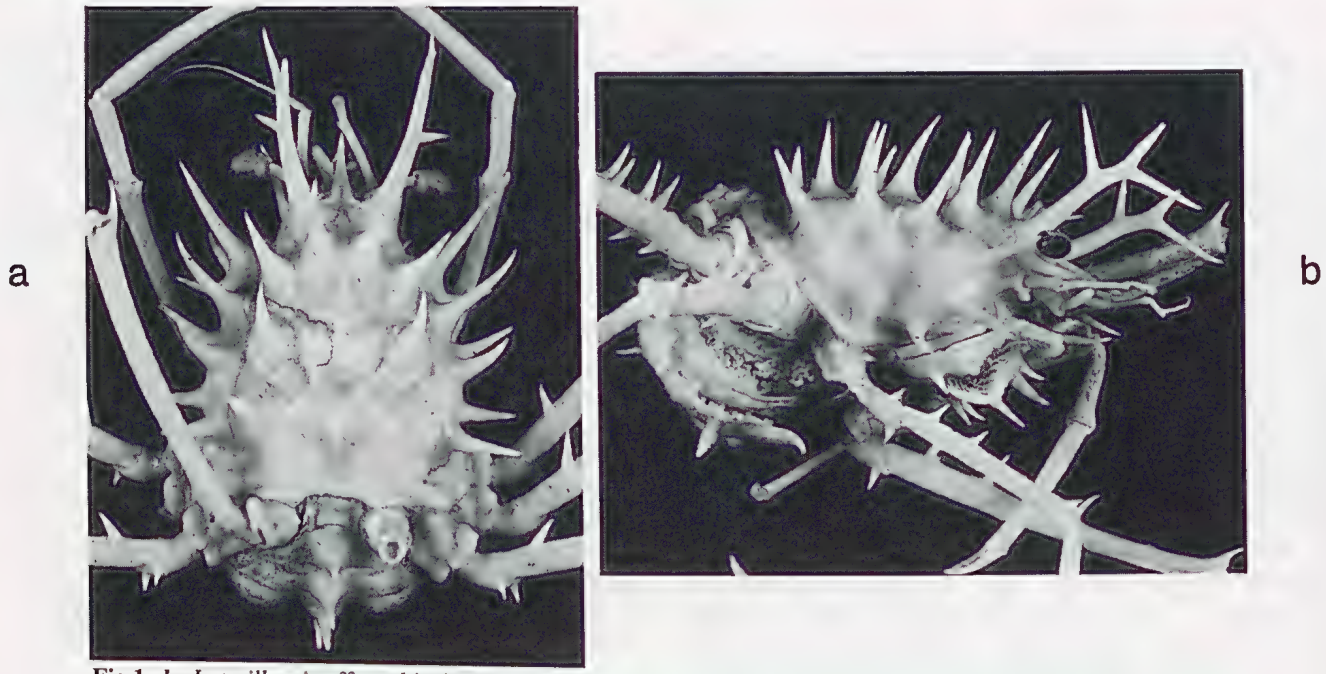

Fig.1a,b. *Latreillopsis* aff. *multispinosa*. a: female, 29 x 28.4 mm, AM P39432, dorsal view; b: same specimen, lateral view.

Gastric area is very wide, separated from the cardiac zone by an overhanging thin plate rising above the cardiac zone. This plate begins at the level of the prebranchial zone and rises progressively; it is widest in its middle and is prolonged by a longitudinal plate on the cardiac zone. Flat branchial and hepatic zones; gastric and cardiac zones slightly bulging. A few bristles on the carapace.

The basal antennal article is short and has several small blunt teeth on its distal edge. The second article is very widened and spread out leaf-like, edged with large spatulate bristles which increase even more its surface. The rest of the antenna is extremely thin and minute; the antennal whip is roughly 1.5 times longer than the second article. The whole of the antenna is shorter than the antennula.

The ocular peduncles are relatively long and present a constriction before the eye which is spherical and pigmented in black. The buccal frame is quadrangular, the third maxillipeds are wide and leave very little space between them; the inner edge of the ischium has long bristles.

The abdomen, very broadened in the ovigerous female, has seven segments.

The chelipeds are shorter than pereiopod 2; the merus is curved and widens distally, it has on its external face a few large bristles. The propodus is swollen and long, the fingers are as long as the rest of the propodus; the fingers have long teeth which mesh together perfectly when the claw is closed.

The ambulatory legs are long and slender, cylindrical in cross-section; the merus of pereiopods 2 to 5 carries strong bristles especially in the distal third; the carpus and the propodus have bristles of varied sizes, some short and crooked, others long and straight; the dactylus which measures two thirds of the propodus is curved and has bristles on its internal edge; the curve of the dactylus of pereiopod 5 is stronger than those of the other pereiopods.

Remarks. The majority of the species of the family of Hymenosomatidae are found in the South-west Pacific, and more particularly around New Zealand and the eastern and southern coasts of Australia. The works of Melrose (1975) and Lucas (1980) have clarified the knowledge of this family. In the key of Lucas (1980), the closest species to *H. lucasi* n.sp. is *H. hondai* (Takeda & Miyake, 1971) which is the only species of the genus *Halicarcinus* to possess a long rostrum. However, *H. hondai* is a littoral species from a reef environment, reported from the Great Barrier Reef. It can easily be distinguished from *H. lucasi* n.sp. by the existence of a tuft of bristles at the end of the rostrum, by the presence of a sharp spine at the anterolateral angle, and by a cornea wider than the ocular peduncle.

Halicarcinus lucasi n.sp. can be distinguished from all other species by the following characters: a simple, very long rostrum curved back towards the top; basal antennal article foliated; the absence of anterolateral tooth; and the presence of a lamelliform plate between the gastric and cardiac zones. The majority of the species of the genus *Halicarcinus* are intertidal and circalittoral while *H. lucasi* n.sp. lives in the upper bathyal zone to a depth of 244 m. Melrose (1975) described a species from New Zealand, *H. tongi* which was taken at a depth of 494 m.

Majidae Samouelle, 1819

Inachinae Macleay, 1838

Achaeus Leach, 1817

Achaeus curvirostris (A. Milne Edwards)

Fig.3a,b

Stenorhynchus curvirostris A. Milne Edwards, 1873: 253.–Haswell, 1882: 2.
Stenorhynchus fissifrons Haswell, 1879: 409.
Achaeus tenuicollis Miers, 1886: 9, pl.1, fig.3a-c.–Whitelegge, 1900: 140.–Rathbun, 1918: 4.

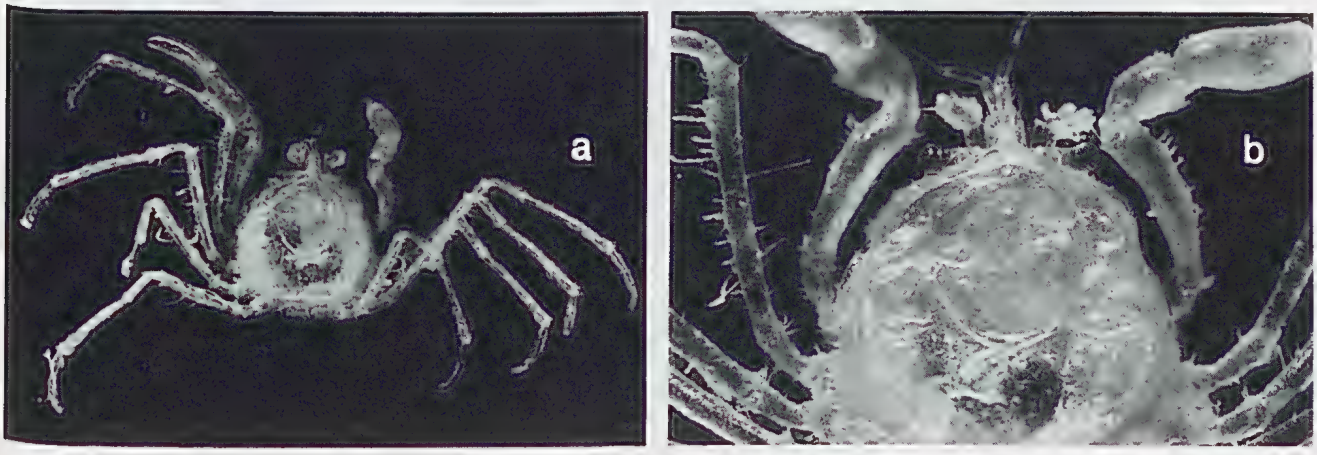

Fig.2a,b. *Halicarcinus lucasi* n.sp. a: female holotype, 2.2 x 2 mm, AM P39429, general view; b: dorsal view.

Achaeus fissifrons.–Griffin & Yaldwyn, 1965: 38-43, figs 1-8.–Griffin, 1966: 38, fig.5.
Achaeus curvirostris.–Griffin, 1974: 4.–Griffin & Tranter, 1986: 9.–McLay, 1988: 118, fig.26.

Material examined. 1 female, ovigerous, 5.4 x 4.5 mm, AM P39424, Gascoyne Seamount, Tasman Sea, 36°43.11'S 156°E, 143 m, 1 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 4. 1 male, 4 x 3 mm, AM P40739, Taupo Seamount, Tasman Sea, 33°14.57'S 156°09.59'E, 131 m, 1 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 6.

Remarks. This species has been reported several times from the east and south coasts of Australia. The specimens from HMS *Challenger* described by Miers (1886), under the name of *A. tenuicollis* came from stations 161 and 162 situated through 38° to 39°S and 144° to 146°E, that is to say, the same latitude as our collection in Bass Strait. The specimen cited by Rathbun (1918) also comes from Bass Strait, while those of Whitelegge (1900) come from the coasts of New South Wales. This species is also known from North Island of New Zealand.

Achaeus sp.

Fig.4a,b

Material examined. 1 female, ovigerous, 5.6 x 4 mm, AM P40747, Britannia Guyot, Tasman Sea, 28°17.04'S 155°36.46'E, 425 m, J.K. Lowry *et al.* on RV *Franklin*, stn 46.

Remarks. This female specimen, in bad condition, does not match any of the species cited by Griffin & Yaldwyn (1965) or Griffin (1966a; 1970), and according to the key of Griffin & Tranter (1986), it should be placed beside *A. akanensis* Sakai, 1938. This species therefore seems new. Although it is not possible to describe it on the basis of so little material, the principal characteristics are given here.

The rostrum is short and divided into two teeth by a very open V, the rostral teeth end in a spiniform tubercle. The supraocular edge carries a strong spine directed frontwards, followed posteriorly by a smaller spine. The neck is short and very constricted. The carapace, which quickly widens after the neck, has well-defined zones. The hepatic zone is composed of a granulous bulge. The branchial zone has a tooth on its edge and a few tubercles on its mesobranchial part as well as hooked bristles; the metabranchial zone is supplied with a strong spine pointing obliquely towards the outside. The cardiac zone is surmounted by a very long spine with a rounded tip. The gastric zone also has a very long mesogastric spine with a rounded tip and a protogastric spiniform tubercle.

The basal antennal article has two spines, subdistal, pointing ventrally. The epistome is smooth. The first segment of the abdomen has a strong, sharp spine turned toward the back.

The carpus and the merus of the chelipeds are spinular. The dactylus of the pereiopods are long and moderately arched.

Macropodia Leach, 1814

Macropodia trigonus n.sp.

Fig.5a-c

Material examined. HOLOTYPE, female, 4.5 x 3 mm, AM P40740, Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, 244 m, 2 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 8. 1 female, completely crushed, AM P39420, 29°13.20'S 160°35.25'E, 1550 m, 4 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 20. 1 female, 7.5 x 5.5 mm, NZOI, Norfolk Island,

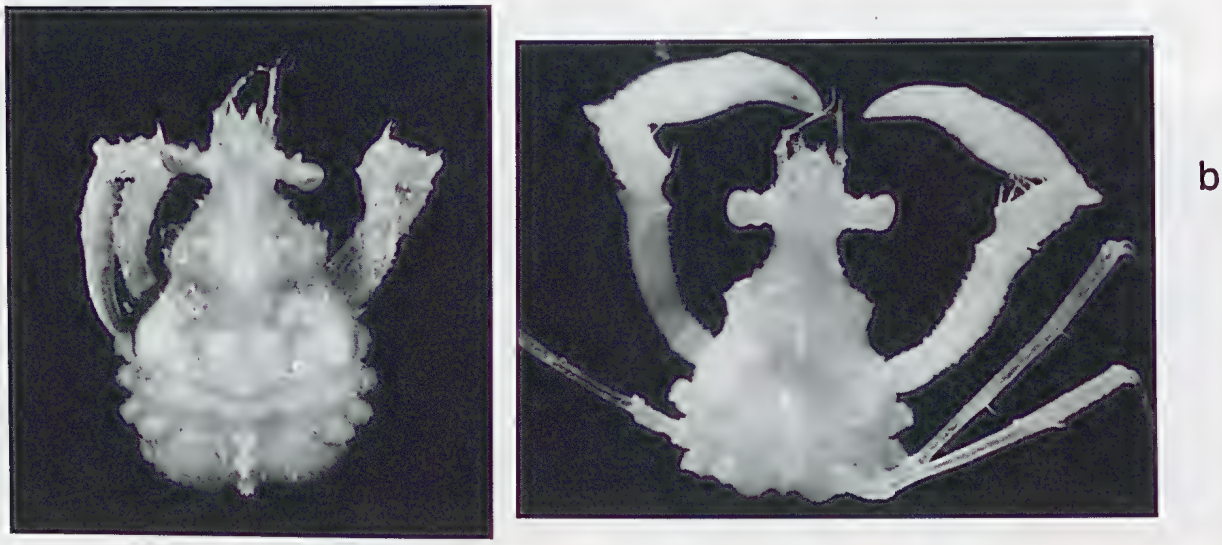

Fig.3a,b. *Achaeus curvirostris*. a: female, ovigerous, 5.4 x 4.5 mm AM P39424; b: male, 4 x 3 mm, AM P40737.

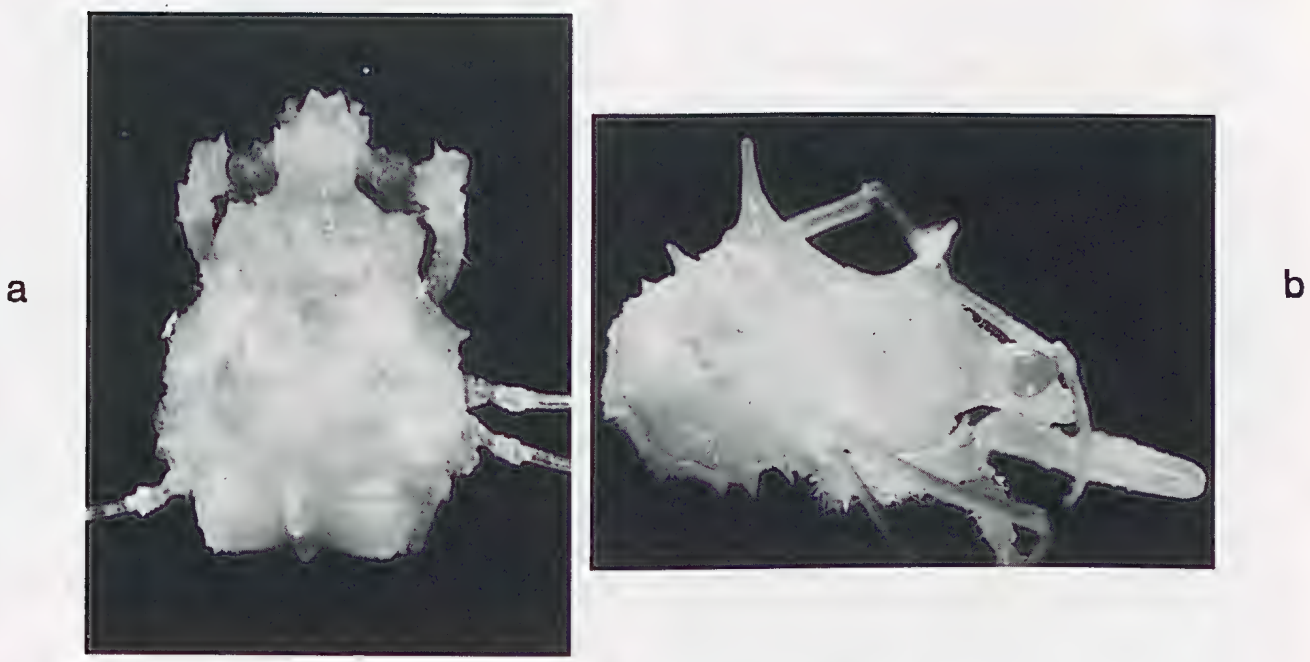

Fig.4a,b. *Achaeus* sp., female, ovigerous, 5.6 x 4 mm, AM P40747. a: dorsal view; b: lateral view.

Fig.5a-c. *Macropodia trigonus* n.sp., female holotype, 4.5 x 3 mm, AM P40740. a: general view; b: dorsal view; c: rostrum and ocular peduncles.

29°07.9'S 168°15.0'E, 280 m, stn I 85.

Etymology. By reference to the triangular shape of its carapace.

Description. Triangular carapace having a few strong spines; neck not very extended and long ocular peduncles; pereiopods extremely long and slender, more than five times the width of the carapace.

The rostrum is composed of two short, coupled spines, having a few spinules laterally. The supraocular eave has a single not very sharp tooth pointing vertically, it grows wider anteriorly as it joins the base of the rostrum. The neck is long and thin and has a spine in front of the hepatic zone. The hepatic zone is very prominent and triangular. It has two small spines on its anterior edge, and ends in a point. A groove separates the hepatic zone from the branchial zone. The branchial zone is very wide with well-defined areas; the epibranchial zone has a spiniform tubercle as well as the mesobranchial zone. The cardiac zone, very extensive, has spine standing vertically; this very broad spine seems to be divided longitudinally. The gastric zone, swollen, has a strong mesogastric spine and some protogastric granules.

The basal antennal article, very long and thin, has three spines: one small proximal, one strong median spine, and one small subdistal spine. This article is compressed laterally. The ocular peduncles as long as the neck, have two spines on their upper edge; the cornea is rounded and has a small horn pointing upwards. The epistome is long and bare. The external angle of the buccal frame forms a foliated expansion edged with three spines. The third maxilliped has four spines on its upper face, one on the ischium and three subdistal on the merus.

The female abdomen is short and broad, having three parallel rows of tubercles, one median and two lateral; six segments are visible. The chelipeds, much shorter than the pereiopod (about one quarter), are slender; the merus, of triangular section, has two spines on its upper edge and one spine on its distal end. The carpus is relatively long and has one spine on its upper edge and a small distal spine, its internal edge is slightly carinated and accentuated by a row of strong spines. The propodus is thin and slightly compressed; the fingers of the claw are thin and subparallel, slightly curved back towards the inside of the hand.

The ambulatory legs, pereiopods 2 to 4, are very long and thin; they have hooked bristles. The merus measures about 2.5 times the width of the body; the carpus and the propodus have bristles on their internal edge. The dactylus, equal to two thirds of the propodus is thin and tapering, rectilinear for three quarters of its length with its distal section slightly curved back. Pereiopod 5, shorter than other legs, presents a short falciform dactylus.

Remarks. This splendid species is easily distinguished from those described by its triangular silhouette and its very long pereiopods.

Until now, few species of the genus *Macropodia* were known from the Indo-Pacific. Griffin (1974) reported two species from South Africa: *Macropodia formosa* Rathbun, 1911 and *M. intermedia* Bouvier, 1940. None of them resemble *M. trigonus* n.sp. *Macropodia formosa* does not carry any spines on its basal antennal article while there are three of them in *M. trigonus* n.sp.

In *M. intermedia* the upper distal edge of the propodus of the pereiopods is spinular while it is inermous in *M. trigonus* n.sp.

Griffin & Tranter (1986) cite in the key to the genus for the Indian Ocean the species *Macropodia falcifera* reported by Barnard (1950) from South Africa. This species is characterised by very long rostral spines which differentiate it from *M. trigonus* n.sp. *Macropodia trigonus* n.sp. is thus the first species of this genus reported from the Pacific. Its small size and its habitat in the bathyal zone explain how it has escaped collection until now. The taking of this species at 1550 m at station 20 is strange; it is probably the case of a specimen which remained attached to the dredge net from the previous station.

Majinae Balss, 1929

Leptomithrax Miers, 1876

Leptomithrax tuberculatus (Whitelegge)

Fig.6

Paramithrax tuberculatus Whitelegge, 1900: 146, pl.34, figs 1-2.

Leptomithrax tuberculatus.–Rathbun, 1918: 22.–Bennett, 1964: 53.–Griffin, 1966a: 285.–Griffin, 1966b: 72.–Griffin & Tranter, 1986: 208.–McLay, 1988: 166.

Fig.6. *Leptomithrax tuberculatus;* female, ovigerous, 27.2 x 24 m, AM P40741.

Material examined. 1 female, ovigerous, 27.2 x 24 mm, AM P40741, Gascoyne Seamount, Tasman Sea, 36°43.11'S 156°E, 143 m, 1 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 4.

Remarks. This species, described by Whitelegge (1900) from the south-east coast of Australia, has also been taken in waters off Queensland (Rathbun, 1918). Its observed bathymetric distribution is from 20 to 78 fathoms (144 m).

A subspecies exists in New Zealand and in the Kermadec Islands, *L. tuberculatus mortenseni* Bennett, 1964, which presents granular metabranchial and intestinal zones of the carapace, while these are smooth in the Australian species. It has been possible to verify this character from the material preserved in the Wellington Museum.

Leptomithrax depressus n.sp.

Fig.7a-c

Material examined. HOLOTYPE, male, 19.6 x 19.6 mm, AM P39425, PARATYPES, 1 ovigerous female, 16.6 x 16.3 mm, 1 female, 10.8 x 11.1 mm, AM P40742, Gascoyne Seamount, Tasman Sea, 36°43.11'S 156°E, 143 m, 1 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 4.

Etymology. By allusion to its very flattened, depressed carapace.

Description. Species of small size, pyriform and very flattened especially in its anterior third; dorsal face entirely covered with large tubercles regularly distributed which do not mask the areas which are well defined; the spines themselves are granular. A few spines on the carapace; the edges are emphasised by very strong teeth The dorsal face carries some scattered hooked bristles, some grouped in tufts on the tubercles of the branchial areas.

Bifid rostrum with two conical sharp spines, short and slightly divergent; the internal face of the rostral spines covered with long hooked bristles. The edges of the carapace carry: two hepatic spines, the anterior spine being the strongest; four very strong conical branchial spines, facing to the outside, the last is the longest and has a more dorsal implantation than the others. These

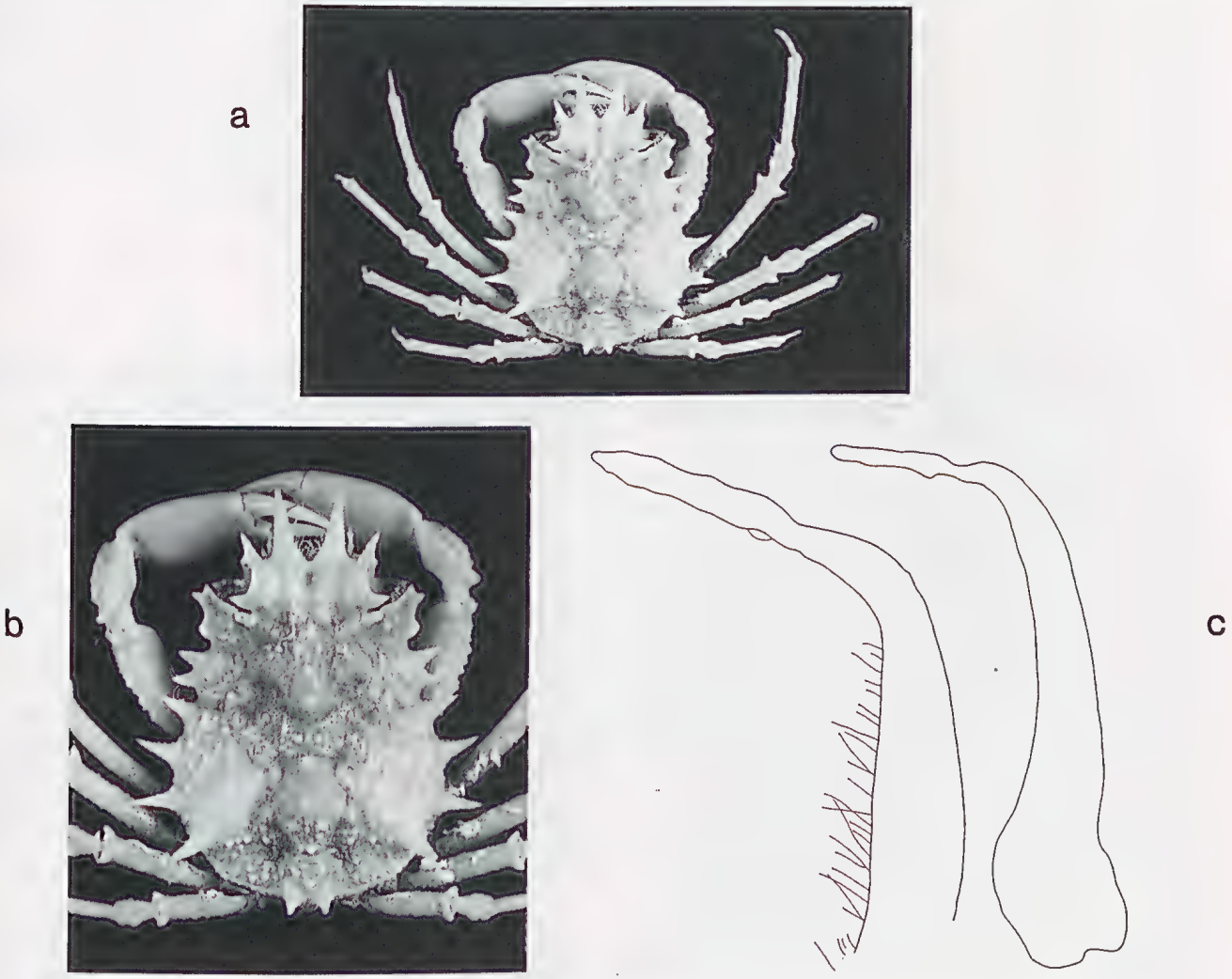

Fig.7a-c. *Leptomithrax depressus* n.sp., male holotype, 19.6 x 19.6 mm, AM P39425. a: general view; b: dorsal view; c: pleopod 1 (length, 3.2 mm).

branchial spines are slightly curved back towards the top at their tip. The posterior edge of the carapace has two short parallel spines pointing backwards.

The dorsal surface has four spines: two on the gastric zone and two on the cardiac zone. On the mesogastric zone, the anterior spine is shorter than the other. One strong spine stands above the cardiac zone which is prominent, and forward of that one there is a small spine.

The orbit is composed dorsally: of a large supraocular eave which ends posteriorly in a foliated spine pointing laterally; of an intercalary rounded spine which rejoins the postorbital spine; of a postorbitary lobe forming a cupel edged with long bristles, divided in two at its extremity and forming a foliated expansion at its posterior edge. The intercalary spine is separated from the supraorbitary edge by a narrow groove and touches the postorbitary spine, it is almost excluded from the orbit. On its ventral face, the orbit is incompletely closed, a broad U-shaped hiatus separate the postorbitary lobe from the basal antennal article.

The ocular peduncles are short, the cornea is wide and topped by a terminal horn. The basal antennal article very developed forms two sharp spines at it upper angles; its ventral face is concave; the spine of its anterior dorsal angle, triangular, is very developed and points towards the front of the animal halfway up to the rostral spine, turned back at its tip, points ventrally. The whole of the ventral face is smooth and punctuated with small holes. The buccal frame is trapezoidal, narrower posteriorly; epistome smooth and depressed.

In the male holotype, the sternum has anterior cavities and longitudinal depressions between each sternite, these depressions grow wider laterally.

The maxillipeds totally cover the buccal frame, the internal edge of the ischium of the third maxilliped with teeth; the ischium is covered with bristles and presents a longitudinal depression; the merus has a concave upper face and an anterolateral angle widened to leaf-shape, the distal edge forms a tooth and a notch.

The chelipeds are short, the propodus is smooth and slightly inflated in the male, the carpus and the merus have their upper face granular. The merus presents an upper edge which is carinated and accentuated with bumps, one spine on the distal edge. The fixed finger of the claw has only one proximal hump which is opposite that of the dactylus. The ambulatory legs are thin and finely granular, pereiopod 2 the longest, the distal edge of the merus from pereiopod 2 to 5 widens forming three blunt teeth. The carpus of pereiopods 2 to 5 is embossed on its external face and presents a longitudinal furrow.

The abdomen is narrow in the male and presents seven segments, the surface of the segments is marked laterally by a hump.

The male pleopod 1 (Fig.7c) is long and thin, globulous at the base, curved back distally and presents a contraction before the opening which is subterminal. The female of 16.6 mm is ovigerous which confirms the small size of this species.

Remarks. The genus *Leptomithrax* has recently been studied by Griffin & Tranter (1986) and according to their key (p.208), *Leptomithrax depressus* n.sp. could be close to *L. bifidus* Ortmann, 1893. This is a Japanese species which lives between 50 to 150 m. However, *L. depressus* n.sp. is easily distinguished from *L. bifidus* by the following characters: there is a single spine on the cardiac zone in *L. depressus* n.sp. and two in *L. bifidus;* in *L. depressus* n.sp. the postorbitary spine is bilobate with a broad foliated expansion, while it is only bifid at its tip in *L. bifidus.*

Leptomithrax depressus n.sp. may be distinguished from all the other species in the genus by its extremely flattened and depressed carapace.

Kimbla Griffin & Tranter, 1986

Kimbla franklini n.sp.

Fig.8a-c

Material examined. HOLOTYPE, male, 6.8 x 4.6 mm AM P39427, PARATYPES, 2 males, 5.7 x 4 mm, 5.2 x 3.8 mm, AM P40743, Taupo Seamount, Tasman Sea, 33°14.57'S 156°09.59'E, 131 m, 1 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 6. PARATYPE, male, 7.2 x 4.7 mm AM P39428, Taupo Seamount, Tasman Sea, 33°14.21'S 156°10.68'E, 133 m, 2 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 7. PARATYPE, male, 8 x 5.5 mm, AM P40744, Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, 244 m, 2 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 8.

Etymology. This species is dedicated to the boat which collected it, the RV *Franklin.*

Description. Species of small size. Pyriform carapace, ill-defined areas, surface of the carapace covered with small granules. Pseudorostral spines pointed and diverging to a V from their base, longer than one third of the length of the carapace, having bristles.

Supraocular eave scarcely widened and having a strong pointed spine facing to the exterior and upwards; a second spine, shorter and slightly curved is found on the posterior edge of the supraocular eave. The intercalary spine is short and pointed, directed upwards, it is clearly separated from the previous one by a U-shape indentation, this intercalary spine is the same size as the posterior spine of the supraocular eave; the postorbitary spine is very long, wide at its base, and has an extra spine situated in the middle of its posterior edge. The base of the postorbitary spine is hollowed by a cupel which eye may lodged. the notch separating the intercalary spine from the postocular spine is narrow. The hepatic zone, barely distended, has a broad, not very pointed spine and posteriorly a spiniform tubercle. The rounded branchial zone is emphasised on its edge by four metabranchial spines facing towards the back. The gastric zone has a small mesogastric spine and two protogastric ones; these spines are small in size and only slightly acerated. The

cardiac zone is topped by two large spiniform granules and the intestinal zone carries three posterior spines pointing backwards of the specimen, these spines are only moderately sharp and are as long as the metabranchial spines.

The basal antennal article is slightly concave, it carries two strong spines on its distal angles, these spines, slightly curved back, point towards the front. The orbit is wide open ventrally, leaving a globulous eye with a short peduncle visible. The eye carries a spine on its upper face.

The third maxilliped is smooth; interior edge of the ischium accentuated with little teeth (10-12); merus carrying a spine at its internal angle.

Chelipeds slightly shorter than pereiopod 2, merus with spinulous tubercles and a distal spine; carpus with a few tubercles and a distal spine; carpus with a few tubercles and a small proximal spine; smooth propodus and not distended in the male.

Ambulatory legs relatively short and thick-set, of cylindrical section, the merus of pereiopod 2 has a distal spine while on the other legs this spine is reduced; all the articles of the legs carry numerous bristles.

The abdomen has seven segments; the sternal plastron is strongly depressed in its anterior part. Pleopod 1 (Fig.8b) has a sharp end with four strong bristles.

Remarks. The genus *Kimbla* Griffin & Tranter, 1986, contained only a single species described from the upper bathyal zone of New Caledonia. The inclusion of *K. franklini* n.sp. in this genus requires a slight change to the definition. The rostral spines of *K. franklini* n.sp. are longer than those of *K. neocaledonica*. The orbit is slightly different: the supraocular eave has two spines in *K. franklini* n.sp. and three in *K. neocaledonica;* the postocular spine is tapered with an accessory spine in

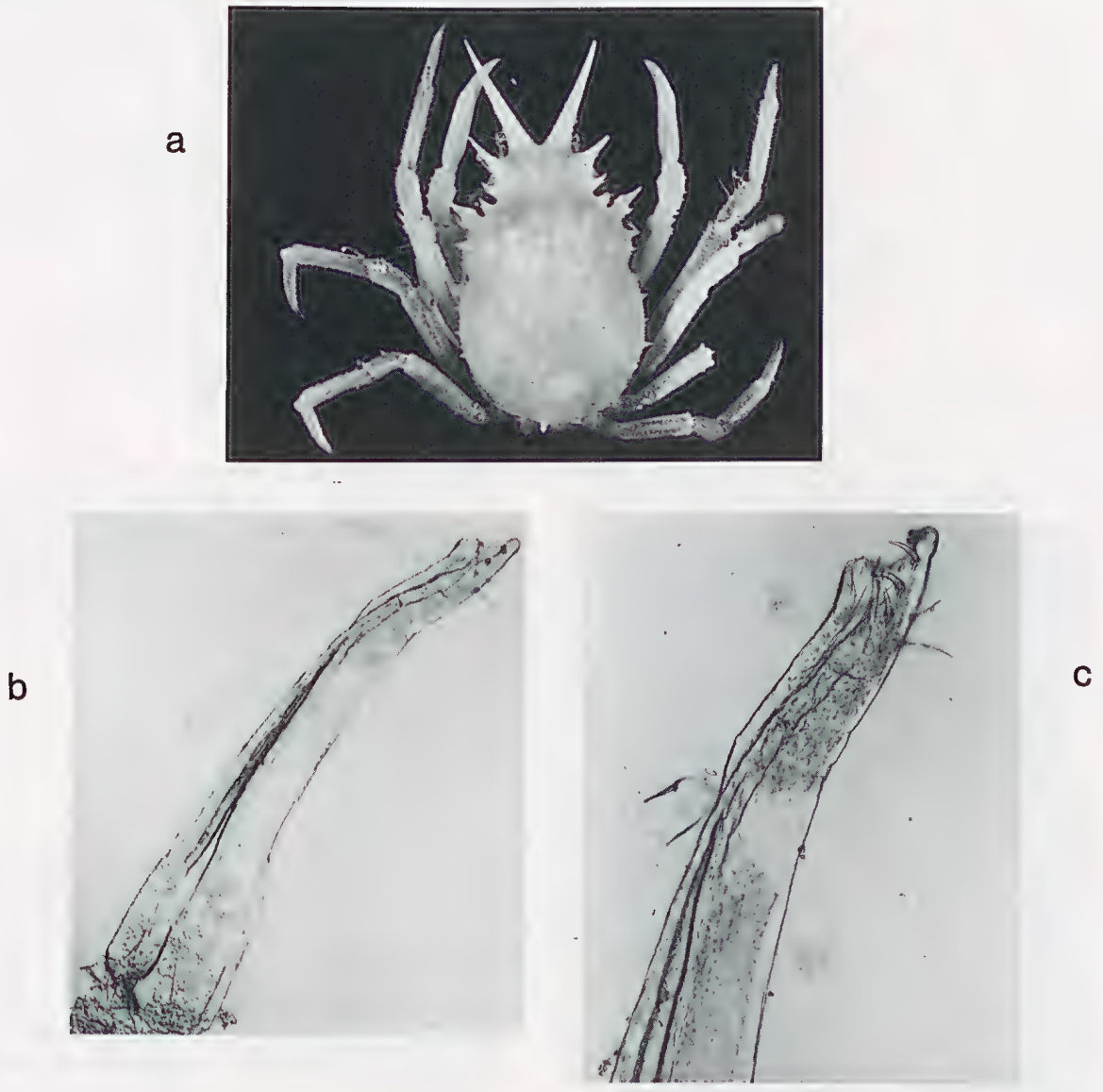

Fig.8a-c. *Kimbla franklini* n.sp., male holotype, 6.8 x 4.6 mm, AM P39427. a: general view; b: pleopod 1 (length, 0.8 mm); c: apex pleopod 1.

K. franklini n.sp. while it is rounded and carries a lateral lobe in *K. neocaledonica*. In the original description, a carapace carrying only granules is mentioned, while the new species carries also spiniform granules and small spines: two hepatic, one mesobranchial, three intestinal, two cardiac, one mesogastric and one protogastric.

Thacanophrys Griffin & Tranter, 1986

Thacanophrys sp.

Fig.9

Material examined. 1 female, 11.4 x 7.2 mm (bad condition), AM P39414, Gifford Guyot, Tasman Sea, 26°43.39'S 159°28.54'E, beam trawl, 295 m, J.K. Lowry *et al.* on RV *Franklin*, stn 38.

Remarks. This small specimen is in a bad condition, the left rostral spine is absent and several spines of the carapace are broken, several legs are missing.

The upper edge of the orbit has two spines; the antorbitary spine is short, slightly curved and indented on its lower edge; the intercalary spine is slender, sharp and indented on its two edges; the postorbitary spine is very long widened at its base with an external edge lamellate; the two hepatic spines are huge and truncate. Two lines of spiniform granules of decreasing size start from the gastric zone and are prolonged on the rostral spines.

The gastric zone, slightly prominent, has two uneven spines, the anterior one being broken at its base on this specimen, the posterior being long and pointing vertically; the cardiac zone has two spines, both broken on this specimen; the branchial zone has two spines (broken on this specimen) and two tubercles topped by a tuft of long hooked bristles; the intestinal zone which carries most probably an uneven spine is completely crushed.

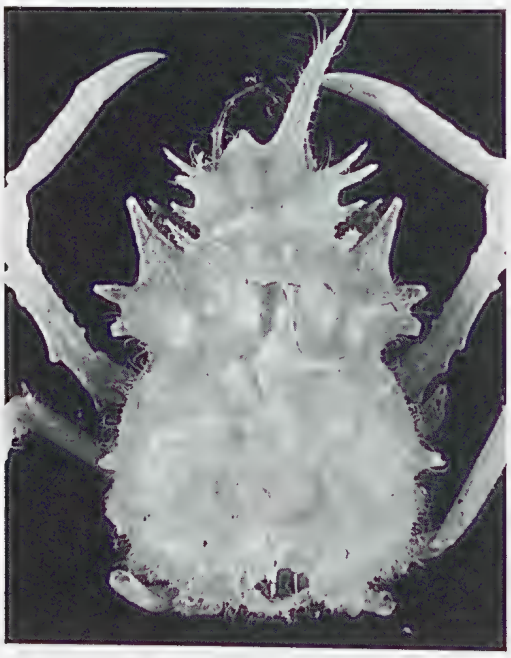

Fig.9. *Thacanophrys* sp., female, 11.4 x 7.2 mm, AM P39414.

The basal antennal article has four long spines, the two external ones protect the ocular peduncle; the cornea is wide and globulous with a strong tooth at its superior face.

On the ventral face, the postorbitary spine presents a lamellate prolongation which borders the orbitary cavity. The upper edge of the buccal frame forms a lamellate crest. The ventral face of the hepatic zone has a lamellate crest which joins the first hepatic spine. The whole of these lamellate crests from the postorbitary spine, from the ventral face of the hepatic zone, from the upper edge of the buccal frame forms a gutter which continues the epistome laterally.

The chelipeds are shorter than pereiopod 2 and slender. The propodus has a crest on its upper edge with a proximal hump; the carpus has two parallel crests consisting of lamellate spines, the proximal spine being the strongest; the merus also has a lamellate crest on its upper edge with two long spiniform expansions on its distal edge.

This species does not correspond to any of those reported by Griffin & Tranter (1986) in their key to the genus *Thacanophrys*. It is probably new and will have to be described using material in good condition.

Pugettia Dana, 1851

Pugettia tasmanensis n.sp.

Fig.10a-c

Material examined. HOLOTYPE, male, 5.1 x 3.6 mm, AM P39426, PARATYPES, 1 male, 5 x 3.4 mm, 2 ovigerous females, 5.2 x 3.8 mm, 5 x 3.8 mm, AM P40745, Taupo Seamount, Tasman Sea, 33°14.36'S 156°09.52'E, 132 m, 1 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 5. PARATYPE, male, 5.6 x 3.9 mm, AM P40746, Taupo Seamount, Tasman Sea, 33°14.57'S 156°09.59'E, 131 m, 1 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 6.

Etymology. After the location of its collection in the Tasman Sea situated between the south-east coast of Australia and the Lord Howe rise.

Description. Species of small size, the largest ovigerous female measures 5.2 mm. Pyriform carapace, practically smooth with the zones poorly defined, barely spinulous. The carapace and the legs entirely covered with short round bristles giving a squamiform look. Rostrum very short composed of two broad flattened spines opened to a V; the base of the rostral spines forming an eave which masks the basal antennal article. The edge of the rostral spines is less than one fifth of the length of the carapace without rostrum.

The orbit is barely shaped and presents a broad gap between the base of the rostral spines and those of the supraocular eave. The supraocular eave is formed entirely

by a broad flat plate, facing the front; the base of this supraocular dentiform eave joins the postorbitary lobe which is poorly developed and rounded.

The hepatic zone is composed of a broad blunt tooth, flattened dorsoventrally, forming an overhang; below this overhang, the hepatic zone presents a hump topped by three tubercles. Edge of the branchial zone having two blunt teeth, the posterior being the longest; a mesobranchial tubercle lightly marked. Cardiac zone marked by a hump as well as the meso and protogastric zones. The intestinal zone is marked by a posterior rim accentuating the edge of the carapace.

The basal antennal article is wide and its anteroexternal angle ends in a spine. The ocular peduncle is short, the eye globulous with a cornea having two small horns, one forwards, one to the back.

The maxillipeds close the buccal frame completely, the internal edge of the ischium of the third maxilliped is indented. The epistome area is slightly concave. The sternum presents a depression forward of the abdomen, which consists of seven segments. The male pleopod 1 is long and thin, slightly distended at its end and ending in a curved beak (Fig.10b).

The chelipeds are inflated in the male with long lateral extensions in the distal part of the propodus; the fixed finger of the claw has six teeth; the dactylus is curved; the carpus and the merus are embossed and the merus is of triangular section and has a spiniform hump on its upper proximal edge. The walking legs are relatively short and thick-set (pereiopod 2 slightly shorter than the cheliped), the articles are of triangular section. The merus of pereiopod 2 carries three spiniform humps, one proximal, one median, one subdistal, and a large distal hump compressed laterally. The size of the legs decreases

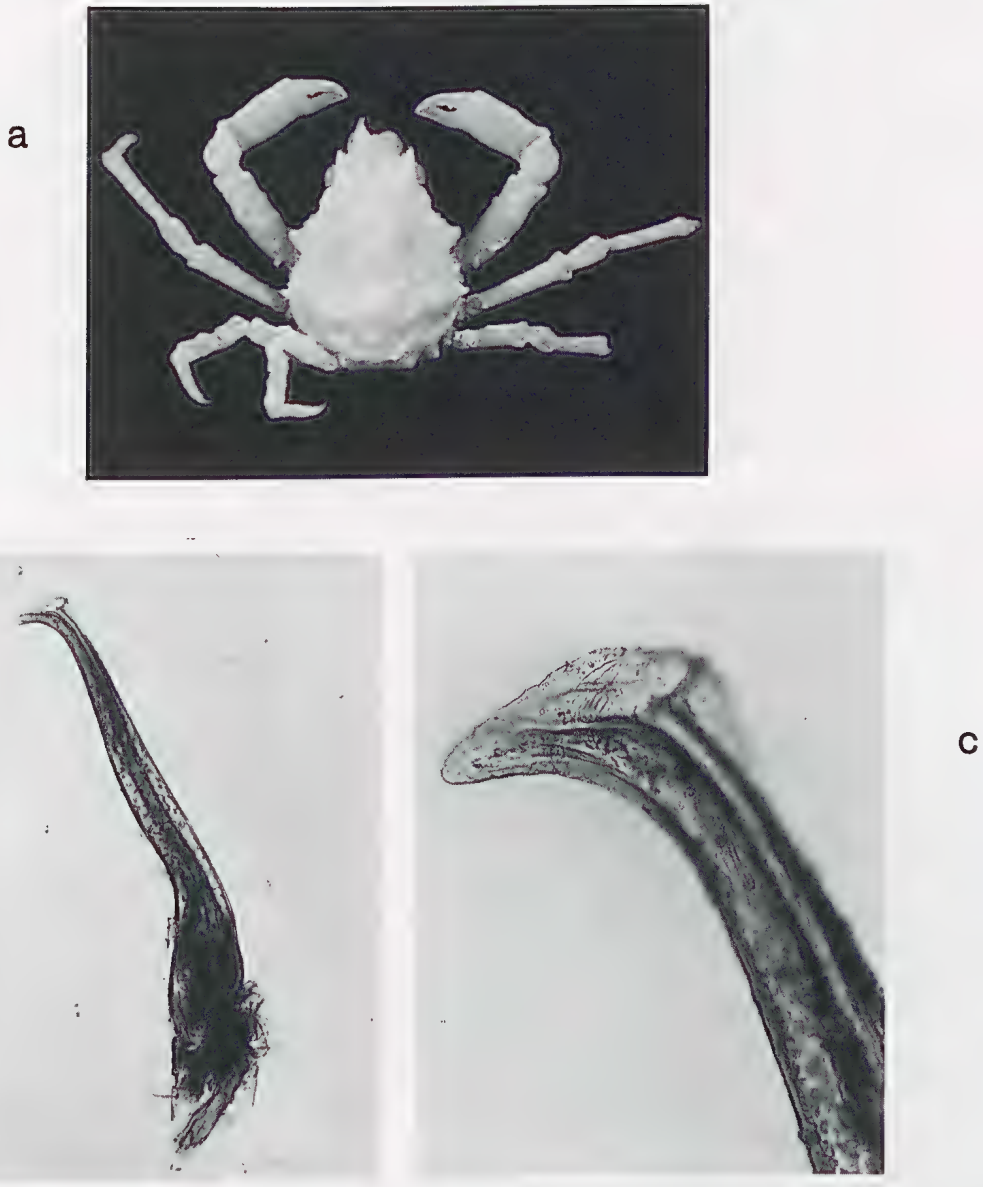

Fig.10a-c. *Pugettia tasmanensis* n.sp., male holotype, 5.1 x 3.6 mm, AM P39426. a: general view; b: pleopod 1 (length, 1 mm); c: apex pleopod 1.

from pereiopods 2 to 5. Pereiopods 4 and 5 which are short and thick have embossed articles and a strong dactylus ending in a hook; the propodus is no longer than the dactylus. The merus of pereiopods 3 and 4 carries only two humps more than the distal hump, the merus of pereiopod 5 has only one, median.

Remarks. It is with some doubt that I place this species in the genus *Pugettia* because the silhouette of its carapace and the shape of its eye, globulous and with two horns, seem to bring it close to the genus *Acanthonyx*. However, the species of the genus *Acanthonyx* are characterised by ambulatory legs modified with subcheliform propodus, which is not the case with *P. tasmanensis* n.sp.

In the genus *Pugettia,* this species is close to *P. quadridens quadridens,* according to the keys given by Sakai (1976) and by Griffin & Tranter (1986). However, *P. tasmanensis* n.sp. is very different from this Japanese species for the following characters: *P. tasmanensis* n.sp. has only one postocular hump while *P. quadridens quadridens* possesses a postocular spine; *P. tasmanensis* n.sp. possesses two spines on its branchial edge while *P. quadridens quadridens* has only one.

Geryonidae Colosi, 1923

Chaceon Manning & Holthuis, 1989

Chaceon bicolor Manning & Holthuis

Fig.11

Geryon affinis.–Griffin & Brown, 1976: 256, figs 7-9.–Sakai, 1978: 9, figs 18,19, pl.2, fig.D.
Geryon quinquedens.–Intes, 1978: 7, figs 5B, 8.–King, 1984: 1986.
Geryon.–Intes, 1978: fig.10.
Chaceon bicolor Manning & Holthuis, 1989: 55, figs 3,4.–Manning, Dawson & Webber, 1990: 604.

Fig.11. *Chaceon bicolor,* male, 41.8 x 61.6 mm, AM P39418.

Material examined. 1 male, 41.8 x 61.6 mm, AM P39418, Lord Howe Rise, Tasman Sea, 29°10.29'S 160°29.78'E, 1509 m, beam trawl, 4 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 21. 1 female, 33.5 x 45.7 mm, AM P39421, Lord Howe Rise, 27°38.8'S 161°46.3'E, 1423 m, beam trawl, 6 May 1989, J.K. Lowry *et al.* on RV *Franklin*, stn 31.

Remarks. The specimens described here are small but the male is no longer a juvenile and its pleopods correspond to the description of Griffin & Brown (1976: 270, fig.9).

The spines of the anterolateral edge are sharp and the spines 3 and 5 are the longest; the upper edge of the orbit is rounded, lightly embossed and presents a slight fissure in its middle; the lower edge has a continuous line of small humps, more distinct than those present on the holotype (Manning & Holthuis, 1989: 69, fig.15a).

On these chelipeds, the palm is inflated and the edges of the fingers of the dactylus and of the propodus have triangular teeth; the carpus is granulous on its external face; the merus has two sharp spines, slightly curved, one distal, the other subdistal. The dactylus of the legs from pereiopods 2 to 5 is compressed laterally.

Colour. When alive, the specimens were uniformly orange-red and not bicoloured. In 1989 we collected in our traps many specimens of *Chaceon bicolor* between New Caledonia and Vanuatu, near Matthew Islands (22°20'S 171°23'E) in depths of 800 m (Laboute *et al.*, 1989). Among these samples, some were mauve and others orangey, but none of them presented a bicoloured carapace. It seems therefore that this character of coloration is not a good characteristic of this species.

Behaviour. During dives with the submersible *Cyana*, carried out in the Loyalty Islands and south of New Caledonia, we were able to observe *Chaceon bicolor* in their environment (Richer de Forges & Grandperrin, 1989). They live on muddy bottoms and have been seen near a burrow; this species appears thus to be able to burrow into the sediment, as has been reported for a South African species *C. maritae* by Melville-Smith (1983) and for the American species *C. quinquedens* by Whitlatch *et al.* (1990).

Distribution. This species has been described recently (Manning & Holthuis, 1989) based on material from New Caledonia. It had been reported from the east coast of Australia by Griffin & Brown (1976) and it is not surprising to find it again on Lord Howe Rise. *Chaceon bicolor* has since been reported from Japan to south-eastern Australia and in New Zealand. It lives between depths of 275 and 1600 m depth; it seems that the juveniles live at a greater depth than the adults. This is mentioned by Manning & Holthuis (1989) and confirmed here, our specimen of small size coming from 1509 and 1423 m. In New Caledonia, the adults are abundant between 600 and 800 m.

Discussion

The insufficient sampling of the Tasman Seamounts does not permit the use of these results for biogeographic comparisons. However, we can see that several species collected on Gascoyne Seamount (36°S) and Taupo Seamount (33°S) are known from South Australia and the North Island of New Zealand; this is the case of *Leptomithrax tuberculatus* and *Achaeus curvirostris*. On the other hand, the sampling from Britannia Guyot (28°S) and Gifford Guyot (26°S) brought up different species: *Thacanophrys* sp., *Achaeus* sp., *Latreillopsis* aff. *multispinosa* and also *Sphenocarcinus lowryi* Richer de Forges, 1991. A better sampling of these seamounts and of the ridges of Lord Howe and Norfolk would no doubt allow us to understand the distribution of the temperate and tropical bathyal fauna.

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On the Status of the Australian Serranid Fishes *Epinephelus ergastularius* Whitley and *E. thompsoni* Whitley

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ABSTRACT. The grouper *Epinephelus ergastularius* Whitley, 1930, from New South Wales and Queensland is recognised as a valid species; it is closely related to the wide-ranging Indo-Pacific *E. octofasciatus* Griffin and the Japanese *E. septemfasciatus* (Thunberg), sharing with them such characters as one or a few small spines on the ventral margin of the preopercle, seven dark bars on the body of the young, the upper half of the peduncular bar black, and the same meristic data, including nine anal soft rays. It differs in having a truncate to slightly emarginate caudal fin in the adult with a distinct broad pale posterior border, pale borders posteriorly on the dorsal and anal fins of adults, and irregular, fine dermal ridges on the back adjacent to the dorsal-fin base. The young can be distinguished by the unequal spacing between the first four dark bars on the body. *Epinephelus chabaudi* (Castelnau) of East Africa is also a close relative, differing in having numerous branched pyloric caeca, a prominent black streak above the maxilla in the adult, and in lacking dermal ridges and broad pale borders on the fins. *Epinephelus thompsoni* Whitley, 1948, is known from a single specimen, taken in 129 to 137 m off Queensland, which has only 13 dorsal soft rays. This grouper name is a junior secondary homonym of *E. thompsoni* (Fowler, 1923). The name, *E. perplexus*, replaced the homonym.

RANDALL, J.E., D.F. HOESE & P. LAST, 1993. On the status of the Australian serranid fishes *Epinephelus ergastularius* Whitley and *E. thompsoni* Whitley. Records of the Australian Museum 45(1): 25–31.

Whitley (1930) described a new species of grouper, *Epinephelus ergastularius*, from a specimen 180 mm in standard length taken in about 15 m near Sydney, New South Wales, in 1925. He gave localities in New South Wales for other specimens in the Australian Museum but did not provide their lengths, registration numbers, or

any indication of their status as paratypes. Under the heading "*Affinities*" he wrote that this species "is apparently closely allied to the Japanese *Perca septemfasciata* Thunberg..." With the possible exception of a smaller eye, none of the characters given by Whitley to differentiate *E. ergastularius* from *E. septemfasciatus* are valid. The colour pattern, general morphology, and meristic data, including nine anal soft rays, are essentially the same. Our first reaction to Whitley's species was to regard it as a probable junior synonym of *E. septemfasciatus*. However, large specimens of a brown grouper from the upper continental slope off northern New South Wales, which were unidentified in the Australian Museum fish collection, have been linked through intermediate specimens to Whitley's *E. ergastularius*. Additional adult specimens from the Coral Sea off Queensland have been obtained from exploratory fishing surveys by the CSIRO. Adult specimens of *Epinephelus ergastularius* and *E. septemfasciatus* have different caudal-fin shapes and colour patterns which led us to recognise them as different species; *E. ergastularius* has a truncate to slightly emarginate caudal fin with a broad pale posterior border, whereas the caudal fin of the adults of *E. septemfasciatus* is rounded and the pale border is either narrow and poorly defined or lacking. Initially we believed *E. septemfasciatus* to be a wide-ranging, deep-dwelling Indo-Pacific species of grouper, but Rudie H. Kuiter informed the senior author that there are two very closely related species of *Epinephelus* in Japan that most authors have confused under the name *E. septemfasciatus*. Katayama in Masuda *et al.* (1984: 132, pl.118A-C) recognised the two, but his characters to differentiate them are largely invalid, and he misidentified the second species as *E. mystacinus* (Poey), a western Atlantic and eastern Pacific fish. The correct name for this species is *E. octofasciatus* Griffin (1926), described from a specimen from New Zealand. The true *E. septemfasciatus* is most easily distinguished by having two narrow close-set dark bars beneath the middle of the soft potion of the dorsal fin instead of a single broad dark bar as in *E. octofasciatus*. From our present knowledge, *E. septemfasciatus* seems to be confined to Japanese waters and may be encountered in SCUBA-diving depths. *Epinephelus octofasciatus* is wide-ranging in the Indo-Pacific; in tropical seas it is generally found at depths greater than 100 m.

We provide below a diagnosis of *E. ergastularius* and differentiate it from *E. octofasciatus*, *E. septemfasciatus*, and another close relative, *E. chabaudi* (Castelnau, 1862) from east Africa.

Whitley (1948) described *Epinephelus thompsoni* as a new species from a gutted specimen ("about 490 mm. in standard length") collected north-east of Cape Moreton, Queensland in 129 to 137 mm; it was deposited in the Australian Museum (AMS E.2116). The mouth of this specimen is wide open, making it difficult to take measurements involving the head. Examination of this specimen revealed that it is a valid species; no other specimens have been found. The name *Epinephelus thompsoni* Whitley, however, is invalid; it is a junior secondary homonym of *Stereolepoides thompsoni* Fowler, 1923, now known to be a junior synonym of *Epinephelus lanceolatus* (Bloch). The name was replaced by *E. perplexus* in Randall & Heemstra (1991). A diagnosis is given for Whitley's fish.

We have examined specimens of *Epinephelus* for this study from the following institutions: AMS – Australian Museum, Sydney; BPBM – Bernice P. Bishop Museum, Honolulu; CSIRO – CSIRO Marine Laboratories, Hobart; NMV – Museum of Victoria, Melbourne; NMNZ – National Museum of New Zealand, Wellington; QM – Queensland Museum, Brisbane; WAM – Western Australian Museum, Perth. In addition, data on specimens of *E. chabaudi* from South Africa have been provided by Phillip C. Heemstra of the JLB Smith Institute of Ichthyology, Grahamstown (RUSI).

Proportional measurements have been rounded to the nearest 0.05. Length measurements of specimens are standard length (SL).

Epinephelus ergastularius Whitley

Figs 1-5

Epinephelus (*Schistorus*) *ergastularius* Whitley, 1930: 119, pl.14, fig.1 (type locality, off Long Bay, coast near Sydney, NSW).

Material examined. AMS IA.2482, 185 mm, holotype of *Epinephelus ergastularius* Whitley, off Long Bay, near Sydney, NSW 15 m; AMS IB.7620, 565 mm, east of Ballina, NSW (28°52'S 153°34'E), 275 m; AMS E.5237, 270 mm, 32 km north of Montague Island, NSW, 108 m; AMS I.23712-001, 625 mm, off Coff's Harbour, NSW (30°41'S 153°25'E), 267-274 m; AMS I.23713-001, 3: 312-402 mm, off Wooli, NSW; AMS I.24504-001, 204 mm, off Bateman's Bay, NSW (35°40'S); AMS I.26022-003, 63 mm, off Woody Head, NSW (29°21'S 153°27'E); AMS I.25865-001, 143 mm, off Port Stephens, NSW (32°49'S 152°07'E), 40 m; AMS I.27362-001, 720 mm, east of Dunk Island, Qld (18°01'S 147°07'E), 300 m; BPBM 30943, 680 mm, off Dunk Island (17°59'S 147°07'E), 320 m; BPBM 31959, 310 mm, northern NSW, 123 m; CSIRO H631-01, 809 mm, east of Dunk Island (18°01'S 147°07'E), 300 m; CSIRO H632-01, 632 mm, east of Dunk Island (17°59'S 147°05'E). 302-308 m; CSIRO H781-01, 545 mm, east of Bowen (19°44'S 152°06'E), 370 m; NMV A5297, 886 mm, east of Dunk Island (18°01'S 147°07'E), 300 m; QM 25660, 781 mm, east of Dunk Island (18°00'S 147°08'E), 298-300 m.

Diagnosis. Dorsal rays XI,14-15 (one of 18 with 15 rays); anal rays III,9-10 (one of 18 with 10 rays); pectoral rays 18-19 (four of 18 with 19 rays); lateral-line scales 63-70; longitudinal scale series 103-116; gill rakers 7-9 + 14-16; pyloric caeca varying from about 30 in a 143-mm specimen (AMS I.25865-001) to 89 in a 680-mm specimen (BPBM 30943).

Body moderately deep for the genus, the depth 2.6-2.9 in SL, and somewhat compressed, the width 1.85-2.35 in depth; head length 2.35-2.55 in SL; snout 3.05-

3.9 in head; orbit diameter 5.6-7.45 in head; interorbital space strongly convex, the least fleshy width 4.55-4.95 in head; suborbital depth 7.9-11.5 in head; least depth of caudal peduncle 3.2-3.9 in head.

Mouth moderately large, the maxilla nearly or just reaching a vertical at rear margin of orbit; upper jaw length 2.0-2.3 in head; dentition typical of the genus (Figs 3,4), the anterior pair of canines not enlarged; 2 rows of teeth on midside of lower jaw, the teeth of inner row longer and depressible.

Posterior nostril ovate and enlarged, 2 or more times larger than anterior nostril; nostrils close together, the posterior flap of anterior nostril reaching posterior nostril when laid back.

The 3 opercular spines broad, very flat, the middle spine much closer to lower than upper spine; posterior preopercular margin finely serrate, the rounded corner fully serrate, the serrae there not or only slightly enlarged; ventral margin of preopercle with 1-4 small downward-projecting spines (often concealed); subopercle and interopercle finely serrate.

Scales on body ctenoid except for nape, thorax, and abdomen; scales on nape and anterodorsally on body very small; no auxiliary scales on body; no scales on maxilla; irregular, fine dermal ridges in a narrow zone on back adjacent to base of dorsal fin (Fig.5).

Third dorsal fin spine usually longest, 2.55-3.2 in head; membranes of spinous portion of dorsal fin deeply incised, the membrane-free distance of third and fourth dorsal spines more than one third (and as much as two thirds) length of spine; scaled basal portion of dorsal fin very fleshy; fourth soft dorsal fin ray usually longest, 2.4-3.5 in head; third anal spine usually longer than second, the second (which can be measured more accurately) 3.1-4.7 in head; second or third soft anal fin rays longest, 2.15-2.9 in head; caudal fin slightly rounded in young, truncate to slightly emarginate in adults; fin length 1.75-2.0 in head; pectoral fins relatively short, 1.65-3.25 in head; pelvic fins 1.8-2.5 in head. All fins becoming relatively shorter, in general, with growth.

Colour in alcohol of juveniles brown with 7 dark brown bars on body which are broader than their paler interspaces; first bar on nape, the last covering most of caudal peduncle (upper half of peduncular bar black); second and third dark bars and fourth and fifth dark bars much closer together than third and fourth bars; dorsal edge of maxillary groove dark brown; median and pelvic fins dark brown; pectoral fins light brown.

Fig.1. Holotype of *Epinephelus ergastularius* Whitley, AMS IA.2482, 185 mm SL, Long Bay, near Sydney, NSW.

Fig.2. Adult of *Epinephelus ergastularius* (photo by Ken Graham).

Colour in alcohol of an adult (AMS IB.7620, 565 mm SL): dark brown without bars; caudal fin and soft portion of anal fin with a broad (7-8 mm) pale yellowish posterior margin; soft portion of dorsal fin with a pale yellowish margin 2-3 mm in width; pectoral fins dark brown, becoming pale yellowish distally (but without having a sharply defined pale border).

A Bishop Museum specimen 310 mm in SL (BPBM 31959) which has well-developed dark bars on the body is just beginning to show a pale margin posteriorly on the caudal fin. A 327-mm specimen (AMS I.23713-001) also has dark bars, a more obvious pale border on the caudal fin, a narrow pale margin on the soft portion of the anal fin and a trace of a pale border on the soft portion of the dorsal fin. Specimens of 452 mm SL and larger lack the dark bars and have more distinct pale borders posteriorly on the median fins.

Colour of large adults from 350 m off Queensland when fresh: pinkish grey with no trace of bars; fins darker than body except for distinct white margins on soft portions of dorsal and anal fins, posterior edges of caudal fin and pectoral fins, and edge of distal half of pelvic fins.

Remarks. Meristic data of *E. ergastularius* above are based on 18 specimens; measurements were taken of 13 specimens, 185-886 mm SL.

Adults of *E. ergastularius* are readily distinguished

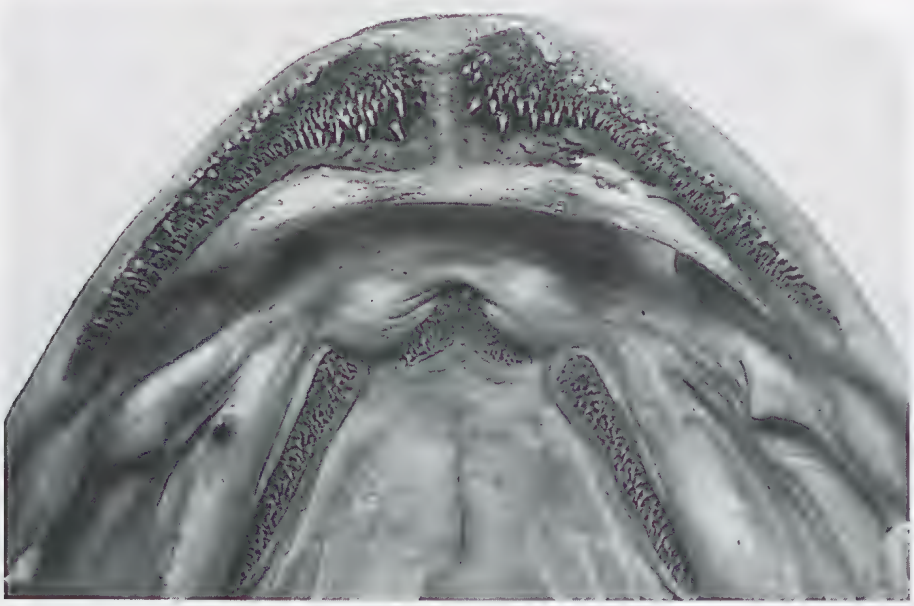

Fig.3. Upper jaw of *Epinephelus ergastularius*, CSIRO H632-01, 632 mm SL.

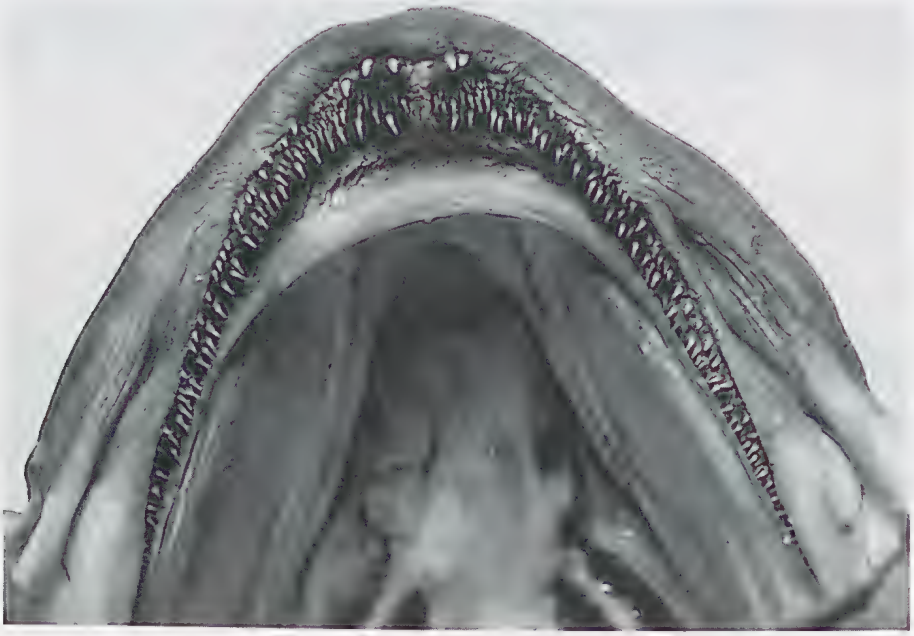

Fig.4. Lower jaw of *Epinephelus ergastularius*, CSIRO H632-01, 632 mm SL.

from *E. octofasciatus* by the truncate to slightly emarginate caudal fin (rounded in *E. octofasciatus*), broad pale margins on fins (absent or narrow on *E. octofasciatus*), and in the possession of the unique dermal ridges next to the base of the dorsal fin. Also on adults the basal scaled portion of the dorsal fin of *E. ergastularius* is more fleshy.

At first, juveniles of *Epinephelus ergastularius* seemed to be indistinguishable from those of *E. octofasciatus*. Both have a dark brown bar on the nape, five on the body beneath the dorsal fin, and a broad one on the caudal peduncle, the upper half of which is black. Then it was noticed that the spacing of the dark bars beneath the dorsal fins is uneven. Designating the bar on the nape as the first, bars two and three are very closely spaced, as are bars four and five. But the pale interspace between bars three and four is about twice as broad as the adjoining pale interspaces. Dark bars two to five on juveniles and subadults of *E. octofasciatus* and *E. septemfasciatus* are approximately evenly spaced. The same spacing is maintained in subadults to a size where the bars are no longer evident. In *E. ergastularius* the second body bar is almost vertical, extending well behind the opercular spine and to above the pectoral base well behind the pectoral insertion; the fifth bar is convex anteriorly. In *E. septemfasciatus* the second body bar curves anteroventrally, with its posterior margin at the posterior end of the opercular spine and ventrally the bar does not extend noticeably beyond the end of the pectoral insertion; the fifth body bar is vertical or slightly convex anteriorly.

We have not examined specimens nor do we know of valid records of *E. octofasciatus* from eastern Australia. This suggests that this species and *E. ergastularius* are allopatric. In view of their obvious close relationship, it is possible that the latter is only a subspecies of *octofasciatus*. However, in view of the differences we have given, we believe they are best regarded as species.

We have data on four lots of *E. octofasciatus* from Western Australia, one of which, AMS I.26027-001, consists of six juveniles, 40-51 mm, taken in 27-51 m off Broome. The other three lots are of single specimens, 240-432 mm, from the Western Australian Museum. The largest, from Rottnest Island, differs in having only a slightly rounded caudal fin. A colour photograph provided by Barry Hutchins of an angler holding a freshly caught *E. octofasciatus* at least 600 mm SL from 80 m at Ocean Reef, WA, has a truncate caudal fin with a distinct white posterior margin that is broader at the corners. Since occasional *E. octofasciatus* have a comparable caudal coloration, and the fish otherwise shows very distinct alternating broad dark brown and narrow white bars typical of the species, we regard it as *E. octofasciatus*. A specimen of *E. ergastularius* of this size would be pinkish grey without bars. However, the truncate caudal fin of this fish suggests that *E. octofasciatus* may have differentiated in Western Australia. Large adult specimens are needed for detailed examination.

The principal difficulty in comparing these various species and forms is the lack of specimens of comparable size from each area. For example, we have only juveniles of *E. ergastularius* from central New South Wales and only subadults and adults from northern New South Wales and Queensland.

Epinephelus chabaudi (Castelnau, 1861) is also a close relative of *E. ergastularius*. It occurs off South Africa to at least 34°S in the depth range of 9-55 m and has been taken off Kenya in 125-200 m (Randall & Heemstra,

Fig.5. Dorsal view of dermal ridges at base of spinous portion of dorsal fin of *Epinephelus ergastularius*, QM 25660, 781 mm SL.

1991). Like *E. ergastularius*, it has nine soft anal-fin rays, one or two small spines on the ventral margin of the preopercle, a truncate caudal fin and close-set nostrils, with the posterior nostril enlarged. Some of the meristic data for *E. chabaudi* are slightly different: soft dorsal-fin rays 13-14 (usually 14); pectoral rays 18-19 (usually 18); lower-limb gill rakers 15-17. The pyloric caeca are numerous, and they are branched. Phillip C. Heemstra counted 30-40 on RUSI 9498, 517 mm SL, each of which has two to five branches. Also *E. chabaudi* lacks irregular dermal ridges adjacent to the dorsal fin, has small scales on the maxilla, and large adults may have some auxiliary scales on the body. In addition, there are differences in colour. *E. chabaudi* lacks pale margins on the fins and has a prominent black streak at the upper edge of the maxillary groove which persists in adults (this streak is less obvious in adults of *E. ergastularius*). The common name for *E. chabaudi* is Moustache Grouper, alluding to this distinctive marking.

Epinephelus ergastularius is known from the eastern coast of Australia between 18°S and 36°S. Our adult specimens were collected in depths from 108 m (specimen from 20 miles north of Montague Island, NSW) to 370 m (east of Bowen, Qld). Juveniles appear to occur in shallower water off New South Wales. The holotype of *E. ergastularius*, for example, was caught in "about 50 feet" (Whitley, 1948). A survey of fishery resources in depths of 200-1200 m in the vicinity of Dunk Island, Qld (17°55'S 146°29'E) resulted in the capture (by trawling and droplining) of specimens of *E. ergastularius* within the relatively narrow depth band of 280-370 m. Its occurrence in shallower depths off New South Wales may be related to the cooler sea temperature there.

The stomach contents of four large adults taken from the FRV "Soela" were dominated by fish remains, including species of *Triacanthodes*, *Argentina* and *Plectranthias*.

Epinephelus perplexus Randall, Hoese & Last

Figs 6, 7

Epinephelus thompsoni Whitley, 1948: 89 (type locality, 58 km north-east of Cape Moreton, Qld).

Epinephelus perplexus Randall, Hoese & Last *in* Randall & Heemstra, 1991: 222 (replacement name for *Epinephelus thompsoni*).

Material examined. AMS E.2116, 465 mm, holotype, north-east of Cape Moreton, Qld.

Diagnosis. Dorsal fin rays XI,13; anal fin rays III,8; pectoral fin rays 18; lateral-line scales 52 (not "about 83" as given by Whitley); longitudinal scale series 104; gill rakers 10 + 17.

Body depth 2.9 in SL; body width 1.6 in depth; head length 2.35 in SL; snout 3.8 in head; orbit diameter 6.0 in head; interorbital space slightly convex, the fleshy width 6.8 in head; suborbital depth 9.5 in head; least depth of caudal peduncle 3.65 in head.

Mouth moderately large: maxilla nearly reaching a vertical through rear margin of orbit, its length 2.3 in head. Dentition typical of the genus; rows of teeth on side of lower jaw, the teeth of the inner row about twice as long as those of the outer row. Posterior nostril ovate, about twice as large as anterior nostril; membranous flap on rear edge of anterior nostril just reaching posterior nostril when adpressed.

Middle opercular spine nearer lower than upper spine; margin of preopercle finely serrate, the corner with a prominent posterior bulge bearing 7 moderately enlarged serrae which seem to be somewhat worn; subopercle and interopercle not serrate.

Scales ctenoid except on thorax and abdomen; no auxiliary scales on body; no small scales on maxilla.

Third dorsal spine longest, 3.25 in head; sixth soft

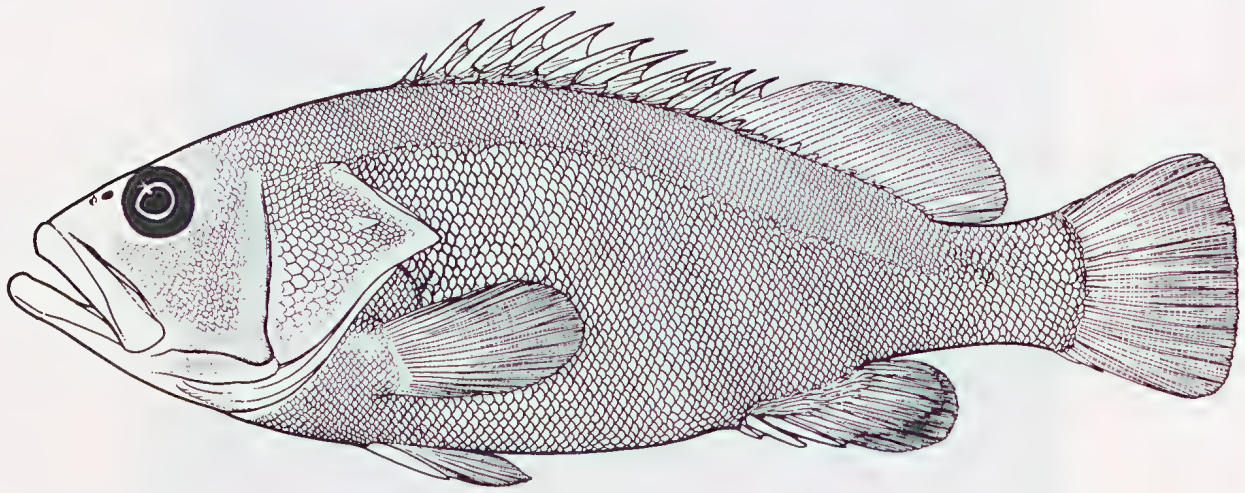

Fig.6. Holotype of *Epinephelus perplexus*, AMS E.2116, 465 mm SL, north-east of Cape Moreton, Qld (drawing by Roger Swainston).

Fig.7. Holotype of *Epinephelus perplexus*, AMS E.2116, 465 mm.

dorsal fin ray longest, 3.1 in head; second anal fin spine 4.1 in head; third soft anal fin ray longest, 2.9 in head; caudal fin slightly rounded, 2.2 in head; pectoral fins not fleshy, their length 2.05 in head; pelvic fins short, 2.5 in head.

Colour in alcohol brown with no obvious dark or light markings. Of the colour, Whitley (1948) wrote, "after long preservation in formalin, light brown. Margins of unpaired fins dark brown. A dark spot on each body-scale. No dark moustache or other conspicuous markings."

Remarks. As mentioned above, *Epinephelus thompsoni* Whitley is a junior secondary homonym of *E. thompsoni* (Fowler). *Epinephelus perplexus* was selected as a replacement name because it seemed odd that only a single specimen of this species is known. The specimen was caught in moderately deep water (the label gives 70-75 fathoms). Because groupers are readily taken by handlines, it is surprising that more specimens have not been found. The lack of additional specimens and the absence of any highly diagnostic characters, apart from the unusual low dorsal soft ray count of 13, is puzzling. Only four other Indo-Pacific species of *Epinephelus* have been recorded with this count: *E. bruneus* Bloch, *E. latifasciatus* (Temminck & Schlegel), *E. radiatus* (Day), and *E. septemfasciatus* (Thunberg) (Randall, 1987). All four have higher lateral-line scale counts (57 or more compared to 52 for *E. perplexus*), and all have dark markings. If the modal soft dorsal fin ray count for *E. perplexus* were 14, 22 other species of the genus in the Indo-Pacific region would need to be compared. All of these are easily distinguished by colour and other meristic data.

Etymology. This species is named *perplexus* due to its many peculiarities.

ACKNOWLEDGMENTS. We thank the crew and captain of the FRV *Soela* for their enthusiastic efforts during fishing operations and, in particular, Wade A. Whitelaw of CSIRO for his assistance in obtaining morphometric, meristic and fishery data. We are also grateful to Tim Fountain and Ms Justine O'Regan for curatorial help, Thor Carter, Ken Graham and Barry Hutchins for photographs; Roger Swainston for the drawing of *Epinephelus perplexus*; and Phillip C. Heemstra for systematic data on *E. chabaudi* and for reviewing the manuscript.

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Taxonomy of *Dendrolagus goodfellowi* (Macropodidae: Marsupialia) with Description of a New Subspecies

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Abstract. Three subspecies of *Dendrolagus goodfellowi* can be distinguished. The nominotypical form is known from two skins and a skull collected in south-eastern New Guinea. *Dendrolagus g. buergersi* (of which *D. g. shawmayeri* is here considered a synonym) is the best represented in museum collections, and is distributed along the Papua New Guinea Central Cordillera, from Wau in the east to Mount Bubiari in the west. *Dendrolagus g. pulcherrimus* n.subsp. is known from a complete spirit specimen, one skin and two skulls collected near Sibilanga in the North Coast Ranges. It is the most distinctive of the subspecies, readily distinguished from all other forms by the broad P^3 with large posterobuccal cusp, orange shoulders, head and ear, pale yellow to white tail rings, white ear margins and pinkish limbs and face. Questioning of local hunters suggests that it is already extinct through most of its original range.

Flannery, T.F., 1993. Taxonomy of *Dendrolagus goodfellowi* (Macropodidae: Marsupialia) with description of a new subspecies. Records of the Australian Museum 45(1): 33–42.

Dendrolagus goodfellowi is one of the smallest members of the genus *Dendrolagus*. A sight record from the Foja Mountains, Irian Jaya by Diamond (1985), and specimens from the eastern Torricelli Mountains here described as a new subspecies, suggests that it was once widespread along the New Guinean North Coastal Ranges. Along the Central Cordillera it is known only from eastern New Guinea; from Mount Bubiari (approximately 15 km east of the Papua New Guinea/ Irian Jaya border) in the west to the mountains of the extreme south-east of the New Guinean mainland in the east (Flannery, 1990; Flannery & Seri, 1990a). *Dendrolagus goodfellowi* occurs in mid-montane oak forest, at elevations of between 1,000-1,200 m and 2,865 m on the Central Cordillera, but extends as low as 680 m in the North Coast Ranges. Its ecology is poorly known, but it is unusual among tree-kangaroos, and indeed among the medium-sized to large macropodids in general, in that it is not sexually dimorphic in size. This study, however, has revealed sexual dimorphism in the extent of convergence of the parietal crests on the skull. It is represented in museum collections by relatively few wild caught specimens and is declining in the wild. Fortunately, however, it breeds readily in captivity (George, 1978; Flannery, 1990).

The taxonomy of *Dendrolagus goodfellowi* Thomas, 1908 has long been confused, partly due to a dearth of specimens. For example Rothschild & Dollman (1936)

had just six individuals (which they divided between three subspecies), while Groves (1982) had only 16, including juveniles and partial specimens. Groves (1982) considered its various subspecies, along with *Dendrolagus spadix* Troughton & Le Souef, 1936, to be forms of *Dendrolagus matschiei* Förster & Rothschild, 1907. More recent research, however, has revealed that *D. goodfellowi* and *D. spadix* probably occur in sympatry in southern New Guinea, and that *D. spadix* is moreover very different in morphology from *D. goodfellowi* (Flannery, 1990). These new data suggest that these two taxa should be considered as distinct species. *Dendrolagus matschiei* of the Huon Peninsula and *D. goodfellowi* of the Central Cordillera and North Coast Ranges are allopatric, but differ in pelage and cranial morphology. Most reviewers have considered them to be distinct species (e.g., Rothschild & Dollman, 1936; Flannery, 1990), although Groves (1982) considered them to be conspecific.

Material here considered as *D. goodfellowi* has usually been divided between three subspecies (e.g., Rothschild & Dollman, 1936; Laurie & Hill, 1954; Groves, 1982; Flannery, 1990). These are *D. g. goodfellowi* Thomas, 1908 from south-eastern New Guinea, *D. g. buergersi* Matschie, 1912 from western Papua New Guinea, and *D. g. shawmayeri* Rothschild & Dollman, 1936 from the Papua New Guinea central highlands.

This work was initiated when a specimen of *D. goodfellowi* was collected near Sibilanga in the North Coast Range of Papua New Guinea. This was the first time that the species had been collected away from the Central Cordillera.

Materials and Methods

Colours where capitalised refer to Smythe (1974). Measurements are in millimetres, and weights are in grams. External measurements were taken in the field. Summary statistics, bivariate plots and t-tests were compiled using STATISTIX. Prefixes for institutions are as follows: AM M – Australian Museum; BMNH – British Museum of Natural History, BZM – Berlin Zoological Museum; MVZ – Museum of Vertebrate Zoology, Berkeley. Only adults (individuals with all molars fully erupted) were included in the cranial measurements. Measurements for the BMNH and BZM specimens were taken from Thomas (1908), Rothschild

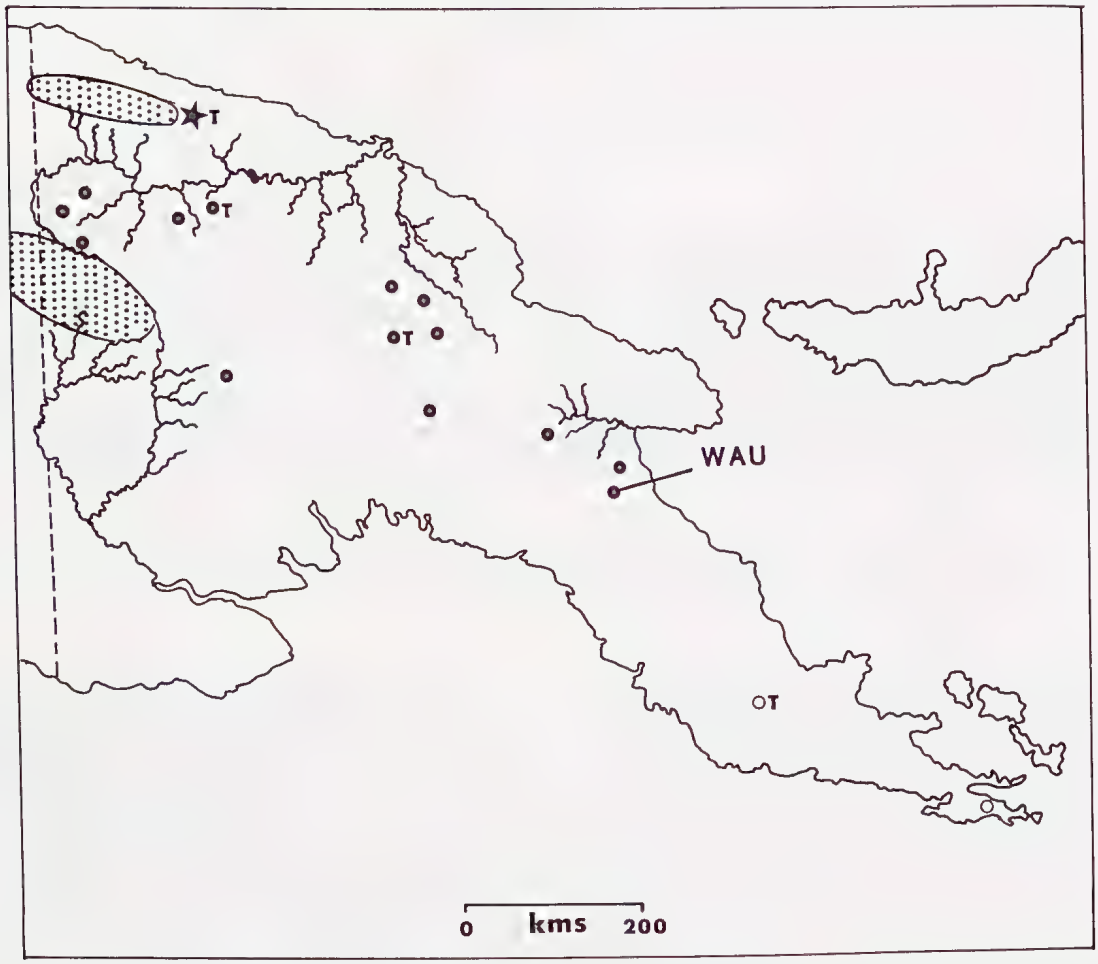

Fig.1. The distribution of *Dendrolagus goodfellowi*. Circle = *D. g. goodfellowi*, dot = *D. g. buergersi*, star = *D. g. pulcherrimus*. Shaded area = regions above 600 m elevation searched by the author and which lack *D. goodfellowi* (see text). T = type locality. The type locality of *D. g. shawmayeri* is the easternmost of the localities marked with a dot and a T.

& Dollman (1936), and Laurie (1952). Those of the MVZ specimens was taken from Lidicker & Ziegler (1968), and these two specimens have not been examined personally by me. The adult AM M specimens examined and used for statistical analysis are listed in Appendix II. Table 1 is listed in Appendix I.

Results

There is considerable variability in pelage from throughout the species range. The features of the pelage that vary most are as follows: 1) pattern of mottling on tail, 2) colour of back, 3) distinctness of dorsal stripes, 4) colour of face and shoulders, 5) colour of limbs. Rothschild & Dollman (1936) placed much emphasis on the pattern of yellow mottling and ringing on the tail. The examination of larger series held at the Australian Museum reveals that these patterns vary enormously between individuals in the only large sample available (that of *D. g. buergersi*), and that they are of no use as a taxonomic character.

Geographic variation in other features is well-marked. Only two skins are known from south-east New Guinea. They differ however from those collected further west along the Central Cordillera in that the back is generally darker, with a buff-coloured speckling not seen in individuals from elsewhere. The dorsal stripes are poorly expressed, with those on the shoulders being almost entirely obscured. The face and shoulders are dark brown. The limbs are likewise dark brown. Two individuals from the Wau area (Fig.1) show essentially similar features, although neither has the buff-coloured speckling of the dorsum. One entirely lacks shoulder stripes, while the other has them poorly expressed (Lidicker & Ziegler, 1968). The relatively large sample available from the Papua New Guinea central highlands (Appendix 1) is relatively uniform in body colouration. The specimens differ from individuals from the south-east in their generally lighter brown back, usually better expressed dorsal stripes (although occasional animals have the stripes muted (e.g., AM M7221), and in having yellow limbs which are sharply offset from the brown body. Animals from west of the central highlands are indistinguishable in pelage from the central highlands sample.

The most distinctive of all the individuals examined are the skin and spirit specimen from near Sibilanga in the North Coast Ranges. They differ from all others examined in that: 1) the tail is ringed with white (in the spirit specimen with a very pale yellow tinge) rather than yellow; 2) the back is Mahogany Red rather than some shade of brown; 3) the throat is white (rather than yellow); 4) the face is pink (rather than brown); 5) the ear rims are white (rather than brown); 6) and the entire shoulder area and crown of the head is Spectrum Orange (rather than brown). They further differ from individuals from the central highlands and the west of Papua New Guinea in that the rump stripes are not as distinct as they usually are in that sample, and in that the limbs are pink and grade into the Mahogany Red of the body, rather than being yellow and sharply offset from the body.

Examination of the skull also reveals geographic as well as sex related variability. Although the sexes do not differ in size, the shape of the parietal crests do seem to be sex related. In old males the crests coalesce to form a ridge on the skull midline, and even in young individuals come into proximity. In females however, they remain separated throughout life, usually not approaching closer than about 0.5 mm, and often up to 10 mm. To assess geographic variation 12 variables were measured (Table 1), and the sample divided into four geographical regions: south-east New Guinea (for which there was a single specimen, the holotype of *D. goodfellowi*), the central highlands (previously recognised as *D. goodfellowi shawmayeri*), west Papua New Guinea (previously recognised as *D. goodfellowi buergersi*), and the two individuals from near Sibilanga in the North Coast Range. The skull of the third Sibilanga specimen was not removed for measuring as it was felt that it was important to keep the animal entire in spirit for future research. A series of t-tests revealed no differences significant at the 0.05 level between the west Papua New Guinea and central highlands samples. Given this result and the great morphological similarity between these samples, they were then pooled for comparison with that from the North Coast Range. Of the eight variables that could be compared, one (P^3 width) was significantly different at 0.05. The great width of P^3 in the North Coast Range specimens is partly due to the great development of the posterobuccal cusp on this tooth. A series of bivariate plots reveals other differences between these populations. P^3 in the North Coast Range specimens is clearly relatively short and broad (Fig.2), while the nasals in this sample are wide relative to the overall width of the rostrum (Fig.3). I could find no other differences in the skull that consistently distinguish the skulls of the three samples under study.

The single adult skull from south-east New Guinea has proved somewhat difficult to analyse. It falls within the range of variability of the central highlands population for all variables except cheektooth row length. In this dimension it is the largest individual known. Further material is needed before the distinctiveness or otherwise of the cranium of this population can be further tested.

This analysis suggests that the division of *D. goodfellowi* from the Central Cordillera into three subspecies is incorrect. There are no consistent differences between samples from western Papua New Guinea (previously called *D. g. buergersi*), and those from the central highlands (previously assigned to *D. g. shawmayeri*). The very poorly known nominotypical population from south-eastern New Guinea does appear to differ consistently from those collected further west, at least in some aspects of pelage. However, only two skins and one skull are known, and some individuals from the Wau area appear to be intermediate between those from the south-east and those from further west

(Fig.1). The most distinctive sample is that from Sibilanga in the North Coast Range. There seems little doubt but that the Sibilanga population represents a form distinct from all others. It is also clear that the populations from western Papua New Guinea and the Papua New Guinea central highlands areas are indistinguishable. The main problem revolves around the very poorly-known nominotypical race from south-east Papua New Guinea. The few data available indicate that they have a distinctive pelage and large teeth. Under these circumstances it seems wise to retain the status quo, and treat the south-eastern form as a distinct subspecies until more material becomes available.

Systematics

Macropodidae Gray, 1821

Dendrolagus Müller, 1840

Dendrolagus goodfellowi Thomas, 1908

Dendrolagus goodfellowi goodfellowi Thomas, 1908

Table 1

Type material. HOLOTYPE, BMNH 8.10.10.1, adult male

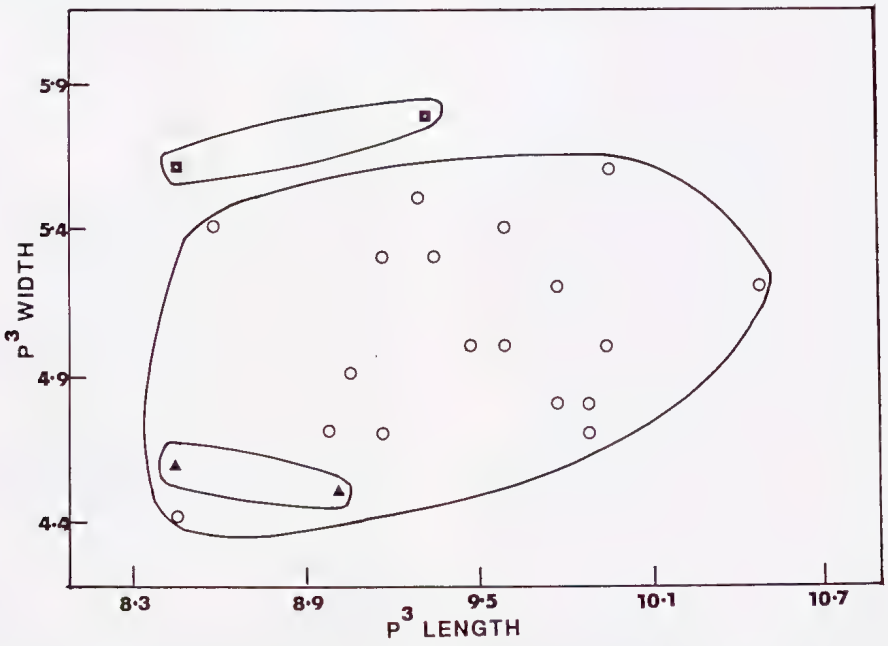

Fig.2. Bivariate plot of P^3 length over width for *D. g. pulcherrimus* (square), *D. g. buergersi* from Wau to Mount Sisa (circles; previously considered to be *D. shawmayeri*), and others (diamond).

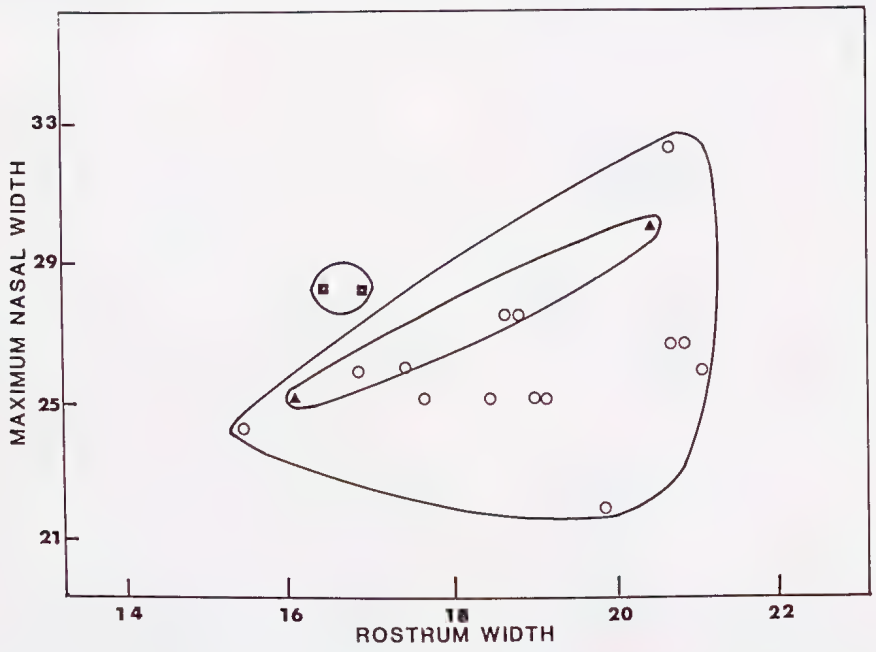

Fig.3. Bivariate plot of maximum nasal width over rostrum width. Symbols as in Figure 2.

skin and skull (broken posteriorly), collected by Mr Walter Goodfellow in 1908 near Mount Obree (9°30'S 148°03'E), Owen Stanley Range, Papua New Guinea (Fig.1).

Diagnosis. Differing from other subspecies in the buff speckling of the pelage and possibly larger cheekteeth. Differing from *D. goodfellowi buergersi* (except those from the Wau area) in having indistinct dorsal stripes, and in having the body colour (brown) extending to the wrists and ankles. Differing from *D. goodfellowi pulcherrimus* n.subsp. in having a yellow (rather than white) throat, brown (rather than pink) face and limbs, brown (rather than white) ear margins, brown (rather than Spectrum Orange) shoulders, brown (rather than Mahogany Red) dorsum, and yellow (rather than white) tail rings, and in having P^3 with less a well-developed posterobuccal cusp.

Discussion. *Dendrolagus goodfellowi goodfellowi* remains very poorly known. Only a single specimen, consisting of a skin but no skull, has been collected since the holotype was described. This specimen (BMNH 50.1433) was collected in the mountains of mainland New Guinea to the west of Samarai Island, extreme south-east New Guinea, sometime between 1932 and 1949, by Mr Fred Shaw Mayer (Laurie, 1952; Groves, 1982). Numerous major expeditions have worked in the south-east of New Guinea (e.g., the 1933-1934, 1953 and 1956-1957 Archbold Expeditions), yet have not encountered this species. It may well be rare and endangered.

The Wau area is geographically intermediate between the south-east and central highlands areas of Papua New Guinea (Fig.1). Individuals from this area reported upon by Lidicker & Ziegler (1968) possess a combination of features seen in *D. g. goodfellowi* and *D. g. buergersi*. They are similar to the former in having the limbs coloured the same as the body, and in having the dorsal stripes muted, yet they lack the buff speckling and apparently large cheekteeth of that subspecies. The Wau area may lie in a hybrid zone between these two populations. However, more specimens from this general region are needed before the status of these individuals can be fully determined. Curiously, *Dendrolagus dorianus* is also divided into a south-eastern and central highlands subspecies. In this case however, animals from the Wau area clearly fall with those from the central highlands and the boundary between these two distinctive subspecies lies near Garaina approximately 60 km south-east of Wau (Kawei, 1989). *Dendrolagus dorianus* is generally restricted to higher elevations than *D. goodfellowi*, so gene flow may be more restricted by low points in the Central Cordillera in this species than in *D. goodfellowi*.

Dendrolagus goodfellowi buergersi Matschie, 1912

Table 1

Synonym. *Dendrolagus goodfellowi shawmayeri* Rothschild & Dollman, 1936.

Type material. HOLOTYPE, BZM 22155, adult male skin and skull, collected by Dr Bürgers in August, 1912 in the Hunstein Mountains (4°21'S 138°08'E), north-west Papua New Guinea (Fig.1).

Diagnosis. Differing from all other subspecies in the sharply-defined yellow limbs, which contrast with the brown body, and the yellow dorsal stripes on the shoulders and rump (they occasionally coalesce to run the entire length of the back). Further differing from *D. g. goodfellowi* in lacking buff speckling over the body, and possibly in having smaller cheekteeth. Further differing from *D. g. pulcherrimus* in having yellow (rather than white) throat and tail rings, brown (rather than pink) face, brown (rather than white) ear margins, brown (rather than Spectrum Orange) shoulders, brown (rather than Mahogany Red) back, and a narrower P^3 with a less well-developed posterobuccal cusp.

Discussion. *Dendrolagus goodfellow buergersi* is the best-represented of all the forms of *D. goodfellowi* in museum collections. It is also the only subspecies currently kept in zoos. It is fairly uniform in morphology throughout its range, except for the population near Wau, which shows some features typical of animals from the south-east. There is considerable variability, however, in tail length and colour, and the intensity of the expression of the dorsal stripes. AM M7221 from high elevation (2,865 m) on Mount Jaka is at one extreme of variability in these features. The dorsal stripes are less prominent than in other Australian Museum specimens, and the tail is very short and entirely brown. As this specimen represents by far the highest elevational record for the species, these features could be the effect of altitude. Another possibility is that the specimen is a hybrid, possibly with *D. dorianus*, as this species is dull coloured and has a brownish-black tail. The colouration of the tail is perhaps the most variable feature, varying from brown, through brown with yellow blotches and rings, through to nearly entirely yellow.

When describing *D. g. shawmayeri* from the Papua New Guinea central highlands, Rothschild & Dollman (1936) note that it differs from other forms in having a more crimson tint to the coat, more distinct striping of the anterior of the body, in having the banding on the posterior of the body lighter, in having hands, feet and tail more richly coloured, in that markings on tail differ in being 'more transverse' throughout, in that the buff colour of the tail is more pronounced, and in having the underparts more yellow. They did not specify which features distinguish *D. g. buergersi* from *D. g. shawmayeri*, but none of these features distinguish animals from the Hunstein Range or other parts west of the central highlands population when the larger samples now available are examined.

Flannery & Seri (1990a) have recently determined the distribution of this subspecies in the western part of its range (west of 142°E). They found that the westernmost population is located at elevations above 1,000 m on Mount Bubiari (4°33'S 141°09'E). It is widespread at

elevations above 1,200 m to the north of the Sepik and Ok Om Rivers in the Telefomin area, but it is absent to the south and west of this area (Fig.1). Unless some unusual differential extinction has occurred, this pattern of distribution suggests that the Sepik River has formed a barrier to the dispersal of this species.

Dendrolagus goodfellowi pulcherrimus n.subsp.

Figs 4,5, Table 1

Type material. HOLOTYPE, AM M21717, adult female skin and skull collected by Pavel German and Lester Seri, 9 Mar. 1990, elevation of 1,120 m in the Kukumbau area on Mount Sapau (3°32'S 142°31'E), near Sibilanga, West Sepik Province.

PARATYPES, AM M23423, adult female whole in spirit (gut separated but intact), collected by Veari Kula, 13 Dec. 1990, elevation of 680 m in the Mount Macholp area (3°21'S 142°35'E) near Sibilanga, West Sepik Province. AM M22173, trophy skull (sex unknown), purchased at Parkop Village near Sibilanga in March 1990 by Pavel German and Lester Seri.

Etymology. Most beautiful (L.)

Diagnosis. Differing from all other subspecies in the greater width of P^3, the white (as opposed to yellow) throat and tail rings, white (as opposed to dark brown) ear margins, pink (as opposed to dark brown) face, Spectrum Orange (as opposed to brown) shoulders and crown of head, mahogany red (rather than brown) dorsum, and brown (rather than yellow) feet. Further differing from *D. g. buergersi* in its pinkish (rather than yellow) arms, which gradually merge in with the body colour rather than being sharply offset.

Description. *Skull.* Holotype skull from aged animal, with enamel crowns of all teeth breached by wear. Paratype skull from younger individual with P^3 erupted but no cheektooth crowns breached by wear. Paratype lacks occipital region and zygomatic arches. Description is of holotype, but variation in paratype is noted. Right side of rostrum damaged and partially healed prior to death. Further damage to region occurred at time of capture. Parietal crests very poorly developed, and not approaching closer than 9.5 mm (Fig.5). Parietal crests of paratype approach within 3 mm of each other, even though from a younger individual, indicating that it is probably male. No inflation of frontals. Remainder of skull as in other *D. goodfellowi.*

I^1 largest of incisors; extends further ventrally than I^{2-3}. I^2 smaller than I^3; crown morphology of I^{2-3} obliterated by wear. In paratype I^3 has groove on posterior surface. C^1 large, rectangular in buccal outline. P^3 relatively short, with distinct, large posterobuccal cusp connected to main crest by thin ridge (in paratype posterobuccal cusp is free standing). Main crest with large anterior and posterior cusps, with three smaller cuspules placed between. Posterolingual cusp large, giving rise to lingual cingulum that terminates just posterior to anterior cusp of main crest. P_3 relatively short and thick, with small posterobuccal and lingual ridgelets. Other features largely obliterated by wear. Molars brachydont, similar in morphology to those of other *Dendrolagus goodfellowi.*

Skin. Dimensions taken in the field as follows (holotype first, spirit paratype next): head-body length = 585 mm, 630 mm; tail-vent length = 725 mm, 710 mm; hindfoot length (s.u.) = 115 mm, 120 mm; ear length (n.) = 54

Fig.4. Captive adult male of *D. g. pulcherrimus*, caught in the Weigin area, Torricelli Mountains, PNG. Photo T. Flannery.

mm, 54 mm; weight = 7,100-7,200 g, 7,000 g. In holotype both nipples enlarged. Claws of hands and feet close to Kingfisher Rufus, thus lighter than in other *D. goodfellowi*; pads of hand and feet yellow/white; throat covered in short white hairs; forearms and feet not matching any colour in Smythe, but admixture of long yellowish and red hairs giving a pink appearance; face overall pinkish in appearance due to intermixing of very short whitish and red hairs and skin showing through; skin of face pinkish white before preparation. Ears with a striking white rim. Inside of ear and small patch at base close to Pratt's Rufus. Chest with a narrow (about 30 mm) longitudinal band of yellowish hairs down midline. Remainder of venter coloured as back. Cloacal region near Orange-Yellow. Shoulders striking Spectrum Orange, with Burnt Sienna mid-dorsal stripe running from hair whorl in middle of back to crown (Fig.4). Back, venter and most of tail close to Mahogany Red. Twinned stripes on rump close to Burnt Orange. Limbs same colour as face, gradually merging into Mahogany Red of body (Fig.4). Tail thinly-furred. Half way down tail are two incomplete whitish bands, followed by four white bands, increasing in width posteriorly. Last 20 mm of tail Mahogany Red.

Spirit paratype (examined before immersion in alcohol) differing from holotype as follows: tail more thickly furred, with three rather than four complete pale tail bands, no incomplete bands; bands with a slight yellowish tinge, Mahogany Red tail tuft, shoulders even more brilliant Burnt Orange, and where they merge into forelimbs a brilliant red band of fur present, orange area of shoulders more extensive posteriorly, almost joining rump stripes. Dorsal stripe even darker and more contrasting with Mahogany Red back.

Discussion. A mammal survey of the North Coast Ranges is now complete. During the survey, which was undertaken from 1985-1990, I was able to determine that *D. goodfellowi* is unknown in the Bewani and Mount Menawa areas in the west of the ranges; and that it no longer exists in the west Torricellis, at least as far east as the Mount Sulen area (3°25'S 142°12'E). A captive specimen, reputedly caught in the Weigin area (3°28'S 142°16'E), was however observed in Karetei Village near Fatima Catholic Mission. The owner reported it to be rare in the Weigin area. Furthermore, during a short visit to the Jayapura area, Irian Jaya, I established that it is unknown in the Cyclops Mountains and the Sentani area. Thus *D. g. pulcherrimus* exists over a small area in the eastern Torricellis, from around 142°16'E to 142°35'E. It probably also exists in the Foja Mountains of Irian Jaya (see below), which is some 400 km to the west of Sibilanga. As it is apparently absent in all intervening ranges (Cyclops, Bewani, Menawa and west Torricelli Mountains) it is likely that it has become extinct in this extensive area in prehistoric and historic times. Currently human populations are very low in this area and abundant apparently suitable habitat exists.

In the densely populated western and central Torricelli Mountains area local Olo speaking peoples remember a tree-kangaroo called *Weimanke*. They describe it as being brown with a pinkish white face. However, the animal has not been seen in their area for about 70 years, and is now considered by them to be extinct (Flannery & Seri, 1990b). I was therefore somewhat surprised to find a population of *D. goodfellowi* in the small Mount Sapau montane block at the extreme eastern end of the Torricelli Mountains. The local name for this species is *Weiman* or *Weimank*, and the description from hunters and congruence of names leaves no doubt but that is the same species as the extinct animal from further west.

Evidence for the existence of *D. g. pulcherrimus* in the Foja Mountains consists of a sighting made by Jared Diamond (personal communication) at an elevation of 1,500 m in the Fojas at 8.00 am on 10 February 1981 in good weather. He observed the animal for 10 minutes at close range as it perched on a branch two m from the ground. (Such an interaction with a wild tree-kangaroo would be impossible elsewhere in New Guinea, but the Fojas are uninhabited and the fauna does not fear Man). The tail and body appeared to be each just under a metre long. The body was rich red in colour,

Fig.5. Skull of AM M21717, holotype of *D. g. pulcherrimus*.

the head pale dull yellow, the face pinker, and the tail yellowish with five dark spots. The arms were red like the body. This description agrees well with *D. g. pulcherrimus*, but differs from all other tree-kangaroos, in the combination of red (rather than brown) body, yellow head, pink face, and arms coloured (approximately) like the body. It differs, however, in tail colour from *D. g. pulcherrimus*, which is Mahogany Red with whitish rings, rather than predominantly yellow with brown spots. This sighting confirms that a form very similar (or identical to) *D. g. pulcherrimus* exists in the Foja Mountains.

The occurrence of a distinctive subspecies of *D. goodfellowi* in the North Coast Ranges poses a zoogeographic riddle, for there is no obvious way that it could have reached these ranges from the eastern part of the Central Cordillera. Cordilleran populations are restricted to 1,200 m elevation and above. *Dendrolagus g. pulcherrimus* occurs as low as 680 m in the North Coast Ranges. *Dendrolagus goodfellowi* does not occur to the west of the Sepik River on the Central Cordillera, although ample habitat exists there (Flannery & Seri, 1990a). This indicates that the North Coast Range population may not have dispersed across the hilly Sepik-Mamberamo corridor which stretches northwards from the Central Cordillera at about 141°E. This corridor rarely rises above 400 m elevation, so it could only have been used by montane-adapted species during glacial maxima. Indeed, it is not certain even at those times that altitudinal zonation was sufficiently depressed to allow species that are currently found only above 680 m elevation to inhabit it. It is possible that this corridor was used, and that differential extinction has removed *D. goodfellowi* from the area to the west of its present range on the Central Cordillera. This would be an unusual pattern of extinction, for the area is sparsely populated, and apparently suitable habitat is abundant. However, given the apparent pattern of extinction in the North Coast Ranges it is a possibility. Another possibility is that the species dispersed from the south or east at some distant period when the Sepik flowed elsewhere, and a hilly corridor linked the Central Cordillera and eastern end of the North Coast Ranges.

The discovery of a population of *D. goodfellowi* in the North Coast Ranges raises the question of the status of *D. matschiei* (which is restricted to the Huon Peninsula, also north of the Central Cordillera). The new subspecies shares a few features in common with *D. matschiei* (such as pale ears and face) but is nonetheless quite distinct. A re-examination of the status of *D. matschiei* is, however, beyond the scope of this work.

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APPENDIX I

Table 1. Summary statistics for samples of *D. goodfellowi*. Although *D. g. shawmayeri* is regarded as a synonym of *D. g. buergersi* here, the samples are kept separate to allow for a statistical comparison. CB = condylobasal length, BZ = bizygomatic width, CT = cheektooth row length, PW = P^3 maximum width, PL = P^3 length, M2 = M^{2-2} external width, NL = nasal length, MN = maximum nasal width, BM = bimastoid width, RB = rostral breadth, RD = rostrum depth, IO = interorbital width.

		D. g. pulcherrimus	*D. g. buergersi*	*D. g. shawmayeri*	*D. g. goodfellowi*
CB	X	107.4	110.6	108.6	115.0
	R	–	103.9-114.1	99.5-119.0	–
	N	1	4	19	1
	STD	–	4.57	4.97	–
BZ	X	63.4	63.0	63.2	67.0
	R	–	60.2-65.5	58.0-68.1	–
	N	1	5	19	1
	STD	–	2.13	2.80	–
CT	X	33.5	33.1	33.7	37.0
	R	32.4-34.6	32.3-34.0	31.0-36.3	–
	N	2	4	16	1
	STD	–	0.79	1.33	–
PW	X	5.7	4.6	5.1	5.6
	R	5.6-5.8	4.5-4.6	4.4-5.6	–
	N	2	2	18	1
	STD	–	–	0.33	–
PL	X	9.0	8.8	9.5	10.0
	R	8.5-9.4	8.5-9.1	8.5-10.5	–
	N	2	2	18	1
	STD	–	–	0.51	–
M2	X	31.9	31.3	30.7	–
	R	30.2-33.5	30.1-32.7	28.4-32.4	–
	N	2	3	14	–
	STD	–	–	1.17	–
NL	X	44.2	43.7	45.2	42.5
	R	43.6-44.8	41.0-45.4	37.5-50.0	–
	N	2	4	17	1
	STD	–	1.91	3.00	–
MN	X	16.9	18.5	18.9	19.0
	R	16.7-17.1	16.3-20.6	15.3-21.3	–
	N	2	2	16	1
	STD	–	–	1.81	–
BM	X	47.1	45.9	46.7	–
	R	–	42.7-49.0	42.3-50.7	–
	N	1	2	13	–
	STD	–	–	2.51	–
RB	X	28.0	28.5	26.0	–
	R	–	24.8-30.4	22.1-31.9	–
	N	1	3	14	–
	STD	–	–	2.18	–
RD	X	26.3	22.2	25.9	–
	R	24.6-28.0	18.0-28.4	23.0-30.5	–
	N	2	4	14	–
	STD	–	–	2.12	–
IO	X	24.3	25.7	24.7	22.0
	R	21.9-26.6	23.7-27.6	20.5-27.8	–
	N	2	2	17	1
	STD	–	–	2.06	–

APPENDIX II

Australian Museum specimens of adult *D. goodfellowi* measured for statistical analysis during this study: *D. g. pulcherrimus* AM M21717 female Mount Sapau Sibilanga area; AM M22173 sex unknown Sibilanga area; *D. g. buergersi* AM M17213 female Thurnwald Range, AM M17222 female Upper Skgonga River (west Sepik Province), AM M17620 male Thurnwald Range, AM M7221 female Mount Jaka Mount Hagen District, AM M7416, AM M7536, AM M7417, AM M7580 females Mount Hagen district (all except AM M7417 via Taronga Zoo), AM M7535 male Mount Hagen District via Taronga Zoo; AM M6509 male Wau district, AM M15721 sex unknown Mount Sisa Southern Highlands Province; AM M5757, AM M7869, AM M7589 females Taronga Zoo (bred from Mount Hagen stock), AM M7999, AM M7574, AM M7568 males Taronga Zoo (bred from Mount Hagen stock).

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A New Species and Two New Subspecies of *Hipposideros* (Chiroptera) from Western Papua New Guinea

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ABSTRACT. *Hipposideros edwardshilli* n.sp., *H. wollastoni parnabyi* n.subsp. and *H. w. fasensis* n.subsp. are described on the basis of electrophoretic and morphological analysis. All are members of the *Hipposideros cyclops* group of Hill (1963). *Hipposideros edwardshilli* is closely related to *H. corynophyllus*. Additional material of *H. corynophyllus* (previously known from a single specimen with broken forearms) is deseribed.

Flannery, T.F. & D.J. Colgan, 1993. A new species and two new subspecies of *Hipposideros* (Chiroptera) from Western Papua New Guinea. Records of the Australian Museum 45(1): 43–57.

Hill (1963) considered that several highly distinctive species of *Hipposideros* belonged within a supraspecific grouping that he called the *Hipposideros cyclops* group. The group as then defined consisted of *H. cyclops* and *H. camerunensis*, both very large species from Africa, and *H. semoni*, *H. stenotis*, *H. wollastoni* and *H. muscinus* from Australia and New Guinea. Hill suggested that it was "...a relict group of remote origin, a view supported by the profound differences between its Ethiopian representatives and its remaining representatives in the Australasian region...". Hill (1963) characterises the Australasian members of the group by their small size, large ears, complex noseleaves and broad skull. Among the distinctive features of the noseleaf Hill (1963) notes the following: the presence of two lateral supplementary leaflets, the intermediate part has a median tubercle and the posterior noseleaf is moderately developed with three supporting septa, its upper edge being more or less semicircular, thickened, and usually having a median club-like process. At the time of Hill's revision the various species were very poorly represented in Museum collections. Hill (1963) had available for study a single specimen each of *H. muscinus*, *H. wollastoni* and *H. stenotis* as well as nine *H. semoni*.

Hill (1985) described *Hipposideros corynophyllus*, based upon a single specimen with both forearms broken. He assigned this new species to the *H. cyclops* group and suggested that it was a close relative of *H. semoni*. He also described three additional specimens of *H. wollastoni* from Telefomin and the nearby Tabubil area, western Papua New Guinea (Fig.1). He noted that the additional *H. wollastoni* specimens all possess a club-like eminence in the middle of the posterior noseleaf, a feature that is lacking in the holotype, until then the only known specimen, which was collected in what is now Irian Jaya, approximately 480 km to the west of Telefomin (Fig.1).

During a survey of the mammals of West Sepik Province T.F.F. was able to collect relatively large numbers of bats referable to the *H. cyclops* group. These included 33 individuals of a new subspecies of *H. wollastoni*, and 24 *H. corynophyllus*, all from the Telefomin area; a single specimen of another apparently new subspecies of *H. wollastoni*, and six individuals of an apparently new species related to *H. corynophyllus*, all from the North Coast Ranges some 200 km north of the Telefomin area. These specimens form the basis of this work. Additionally, four specimens of *H. semoni*, four of *H. stenotis* and one of *H. muscinus*, which had not previously been reported upon, were available for study.

Materials and Methods

Colours where capitalised refer to Smythe (1974). The following prefixes for registration numbers of specimens are used. AM M – Australian Museum; BMNH – Natural History Museum, London; CM – Australian National Wildlife Collection; WAM – Western Australian Museum. The holotypes of *Hipposideros corynophyllus* and *H. wollastoni* were examined by T.F.F during a visit to the Natural History Museum in November 1989. Other specimens examined during this study are listed in Appendix II. Tables 1-4 are included in Appendix I.

Electrophoresis was performed for one hour with a constant 200v potential drop between electrodes on Titan 111 cellulose acetate plates according to standard procedures and stained using agarose overlays following recipes given in Harris & Hopkinson (1977), Richardson *et al.* (1986) and Colgan (1986). Details of running buffers are given in Table 1. Portions of liver were ground in two volumes of homogenising buffer (Colgan, 1986) in hand held glass grinders. The homogenate was centrifuged and the supernatant stored (for up to two weeks) at -75°C until required for electrophoresis. The allozymes identified in this study are designated by numerals in order of decreasing (anodal) mobility. Distance analyses and measures of genetic variability were calculated using BIOSYS-1 (Swofford & Selander, 1981) or by hand. Duplicate loci present in *H. edwardshilli* and *H. corynophyllus* but not in other taxa were included in the calculation of the distance between this one pair but were not used in other calculations. All distance measures available in BIOSYS-1 were examined. The values for the standard Nei distance and Wright's modification of Roger's distance are given in Table 2 (Nei's unbiased estimate cannot be calculated for heterozygotes in single specimen samples, i.e., for *H. w. fasensis* here, so the standard Nei measure is given for distances where one or both taxa have only one specimen).

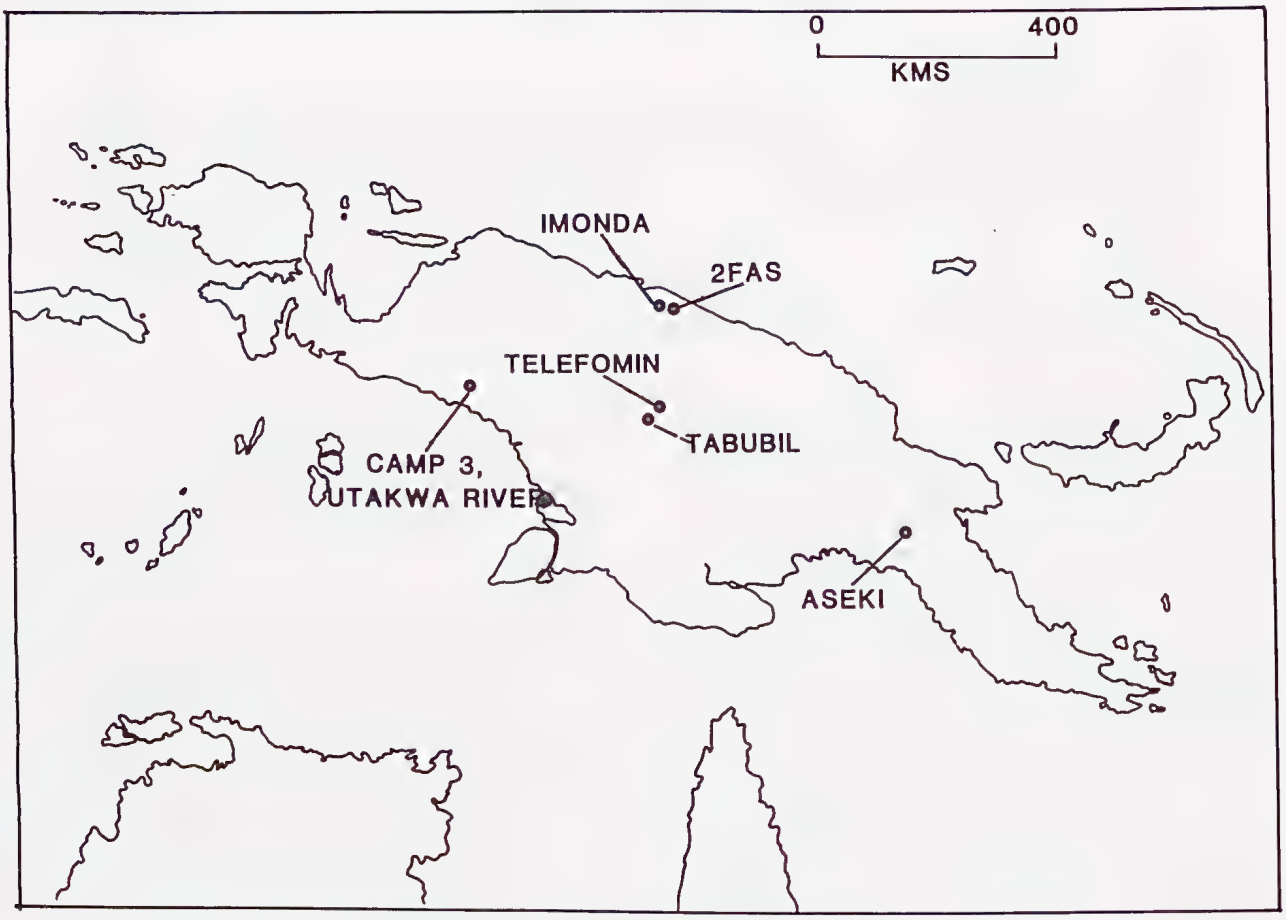

Fig.1. Map of New Guinea showing localities and areas mentioned in text.

Results

Electrophoresis. Genetic studies were made of the following specimens: *H. edwardshilli*, *H. corynophyllus*, *H. w. parnabyi* and *H. w. fasensis*. Studies of 34 presumptive loci show that *H. edwardshilli* and *H. corynophyllus* are distinguished by fixed differences for three isoenzymes (AK-1, MPI-1 and 6-PGDH) and a large frequency difference at another (G-6-PDH-2). The Nei genetic distance between these taxa is relatively small compared to their distances from *H. w. parnabyi* and *H. w. fasensis* and, indeed, if taken at face value, would not strongly suggest that two distinct species are being analysed. However, it may be noted that there is a very low level of genetic polymorphism within both *H. edwardshilli* and *H. corynophyllus*. This would tend to minimise the effect of the variation which is observed between the taxa (owing to the use of the squares of identities within taxa in the denominator of Nei's metric). The factor should not be so apparent in Roger's distance calculations, and as can be seen from Table 2, the value for this distance between *H. edwardshilli* and *H. corynophyllus* is higher than the Nei metric when compared to the measurements between the other taxa. When viewed in this light, the genetic evidence provides support for the separation of *H. edwardshilli* and *H. corynophyllus* into distinct species.

Genetic studies of 31 presumptive loci show that *H. w. parnabyi* and *H. w. fasensis* are distinguished by four fixed differences (FDP, GPI, LDH-1, and UDPG). Examination of more specimens of *H. w. fasensis* might reduce this number but it is more probable that large frequency differences would remain for these isozymes. Further studies could also reveal that the allozymes (IDH-1 2 and PGM 1) which are found in the present sample in *H. w. fasensis* but not *H. w. parnabyi* are actually restricted to the former taxon. In any case the genetic data strongly support the discrimination of these taxa at least at the sub-specific level.

Systematics

Hipposideridae

Hipposideros Gray, 1831

Hipposideros edwardshilli n.sp.

Figs 2-5, Table 3

Type material. HOLOTYPE, AM M21752, adult female in spirit, skull extracted. Collected from a mistnet set at Imonda Station (3°20'S 141°10'E), Bewani Mountains, Papua New Guinea at an altitude of 240 m, 1 Mar. 1990, P. German & L. Seri.

PARATYPES, AM M21753, adult male skin and skull, same data as for holotype; AM M21749, adult female in spirit, skull extracted, AM M21750-51, adult males entire in spirit, all from cave 150 m south-west of Imonda Airstrip, 28 Feb. 1990, P. German & L. Seri; AM M22841, adult female in spirit (skull extracted but not fully cleaned), collected while flying by local people at Pou Village near Imonda by V. Kula, 8 June 1990.

Etymology. In honour of John Edwards Hill, in recognition of his outstanding contributions to bat taxonomy, and the help he has extended over the years to researchers investigating chiropteran taxonomy.

Diagnosis. Differing from all *Hipposideros* except members of the *H. cyclops* group of Hill (1963) in possessing two club-like projections on the noseleaf. The two African members of the *H. cyclops* group are very large and markedly different from the Australasian

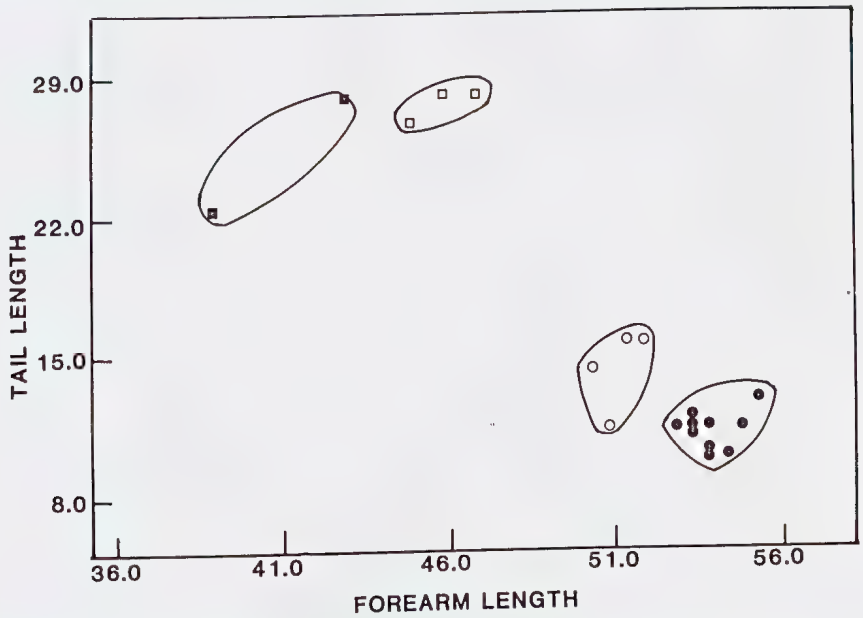

Fig.2. Bivariate plot of tail length over forearm length (in mm) for *Hipposideros corynophyllus* (dot), *H. edwardshilli* (circle), *H. semoni* (hollow square) and *H. stenotis* (square).

species (Hill, 1963) and they are not further discussed here. Differing from all Australasian members of the *H. cyclops* group except *H. corynophyllus* Hill (1985) in having a forearm length greater than 49.6 and a tail less than 15 mm long, in having the postmetacrista of M^3 reduced, and in having the talonid of M_3 reduced and laterally displaced. Further differing from *H. semoni* and *H. stenotis* in lacking the thin web of bone connecting the articular and angular processes on the mandible, in having C^1 and P^4 separated by P^2 (a feature that also distinguishes it from *H. wollastoni*). Further differing from *H. muscinus* and *H. wollastoni* in having the club-like projections of the noseleaf very prominent, and from *H. wollastoni* in lacking an accessory posterior noseleaf. Differing from *H. corynophyllus* in being Prout's Brown dorsally and Cinnamon Rufus ventrally as opposed to Hair Brown overall, and in that: i) the fur and forearm are shorter and the tail on average longer (Fig.2, Table 3); ii) the rostral swellings are more inflated; iii) the frontal concavity is deeper in profile; iv) the postorbital region is more constricted; v) the bulla are on average larger; and vi) the ventral projection of the noseleaf is

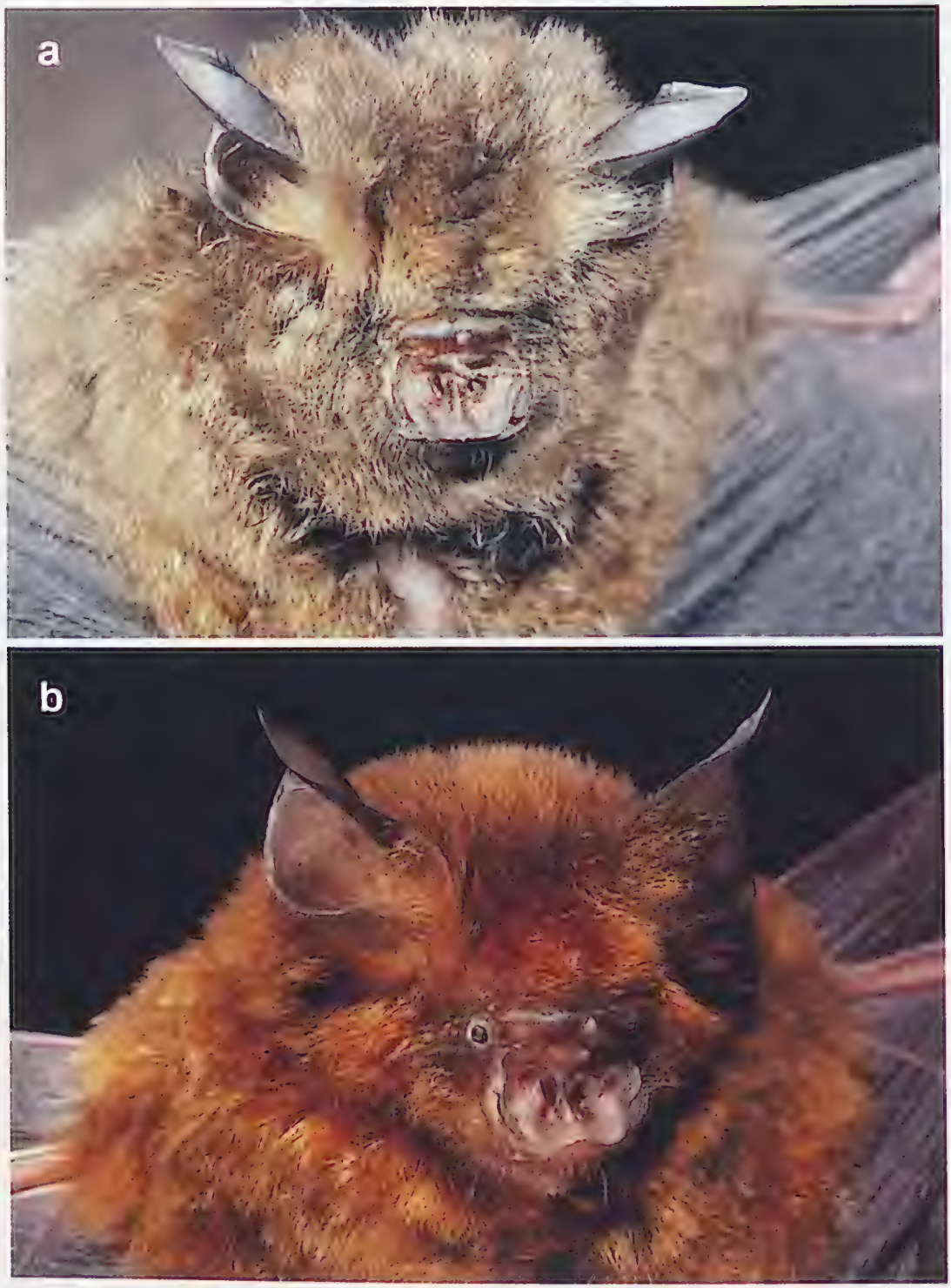

Fig.3. Colour photographs of a, *H. corynophyllus* (photo H. Cogger) and b, *H. edwardshilli* (photo P. German).

shorter and laterally compressed (Fig.3).

Description. Externally most similar to *H. corynophyllus* Hill (1985), but differing in that the fur is Prout's Brown dorsally with a reddish tinge in life, and the venter is Cinnamon Rufus (Fig.3). This presents a marked contrast to *H. corynophyllus* which is close to Hair Brown all over, but with silver tipping ventrally. The fur is also markedly shorter: around 8.7 mm long on the midback on a study skin of *H. edwardshilli*, as

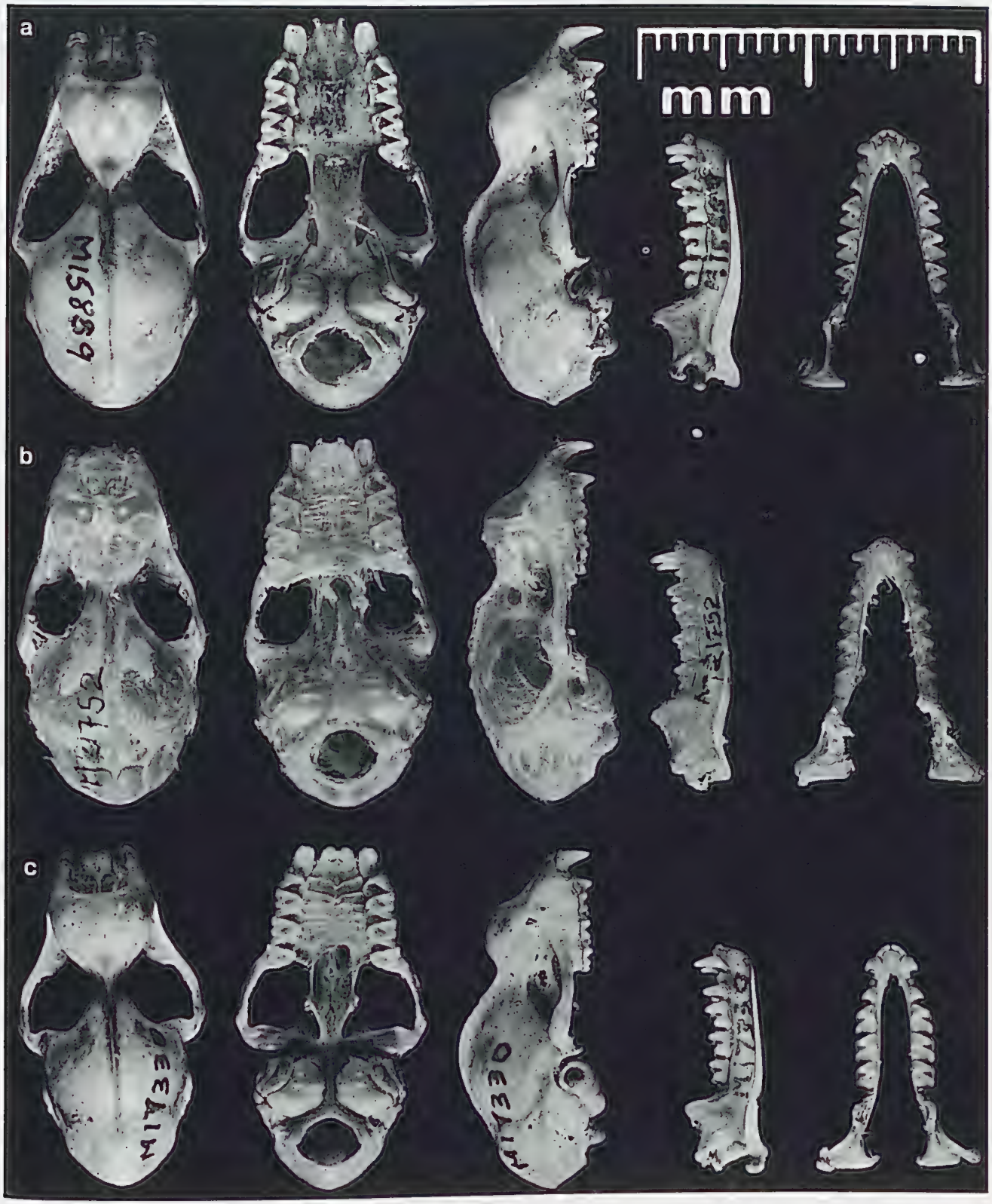

Fig.4. Photographs of the skulls of a, *Hipposideros corynophyllus* (AM M15889); b, *H. edwardshilli* (AM M21752 holotype); and c, *H. semoni* (AM M17330).

opposed to 14.2 mm in the same position in a study skin of *H. corynophyllus*. The claws of the feet of the new species are smaller than in *H. corynophyllus*. The tail is very short (11.1-15.0 mm long). The noseleaf is largely similar to that of *H. corynophyllus*, differing primarily in the shape of the lower club. In *H. corynophyllus* this club is very long and tubular; in *H. edwardshilli* it is shorter and laterally flattened (Fig.3).

In many regards the skull of *H. edwardshilli* is intermediate in morphology between the conditions seen in *H. semoni* and *H. corynophyllus*. The rostral swellings are intermediate in size between the condition seen in these species (Fig.4). Partly as a consequence of this the frontal concavity is in profile deeper than in *H. corynophyllus* but shallower than in *H. semoni* (Fig.4). The anteorbital foramen is elongate and similar in shape to that of *H. corynophyllus*. The bulla are larger than in either species (Figs 4-5). The dentary lacks the thin web of bone that connects the angular and articular processes, as in *H. corynophyllus*. The P^2 prevents contact between the C^1 and P^4, also as in *H. corynophyllus*. The posterior end of the molar dentition is also reduced in a similar manner to *H. corynophyllus*, the postmetacrista of M^3 being minute, while the talonid of M_3 is reduced and laterally displaced (Fig.4).

Discussion. The recovery of a large sample of *H. corynophyllus* has allowed for a re-assessment of the diagnosis of this species as given by Hill (1985) which was based upon a single specimen with both forearms broken. A statistical summary for this sample is given in Table 3. Hill (1985) estimated that the forearm length might have been around 48 to 49 mm. The sample now available indicates that forearm length ranges from 52.0 to 54.6 mm (mean = 53.0 mm). The dental, cranial and facial features as described by Hill (1985) are confirmed by the larger series, but an additional important feature, tail length, has been identified. Tail length ranges from 9.0 to 12.0 mm, which is far shorter than in any other Australasian species in the *Hipposideros cyclops* group. Both forearm length and average tail length distinguish *H. corynophyllus* from *H. edwardshilli* (Fig.2). The inverse relationship between tail and forearm length in the four species in Figure 2 is curious. Such a relationship is not evident in other members of the *H. cyclops* group.

Hipposideros edwardshilli is known from six individuals, of which two are subadult. The subadults are greyish in colouration, while all four adults are brownish red, as described above for the holotype. Three of these specimens were taken from a limestone cave at an altitude of 240 m, and others were caught while flying in the vicinity. *Hipposideros corynophyllus* also inhabits limestone caves, but it is only known from elevations above 1,400 m in the Telefomin area, approximately 200 km to the south (Flannery & Seri, 1990). *Hipposideros corynophyllus* shares caves with *H. wollastoni parnabyi* in the Telefomin area. No *H. wollastoni* were collected in the cave that shelters *H. edwardshilli* near Imonda.

It seems likely than the nearest relative of *H. edwardshilli* is *H. corynophyllus*. Both species have reduced the posterior ends of the molar rows and have very short tails. Both features are unique within Australasian members of the *Hipposideros cyclops* group, and are unusual within *Hipposideros* as a whole. They are also both large species (the largest of the Australasian members of the *H. cyclops* group), and both have very well-developed club-like projections in the centre of the posterior and intermediate noseleaves. It is interesting that in so many aspects of cranial morphology *H. edwardshilli* is intermediate between the condition seen in *H. semoni* and *H. corynophyllus*. These three species,

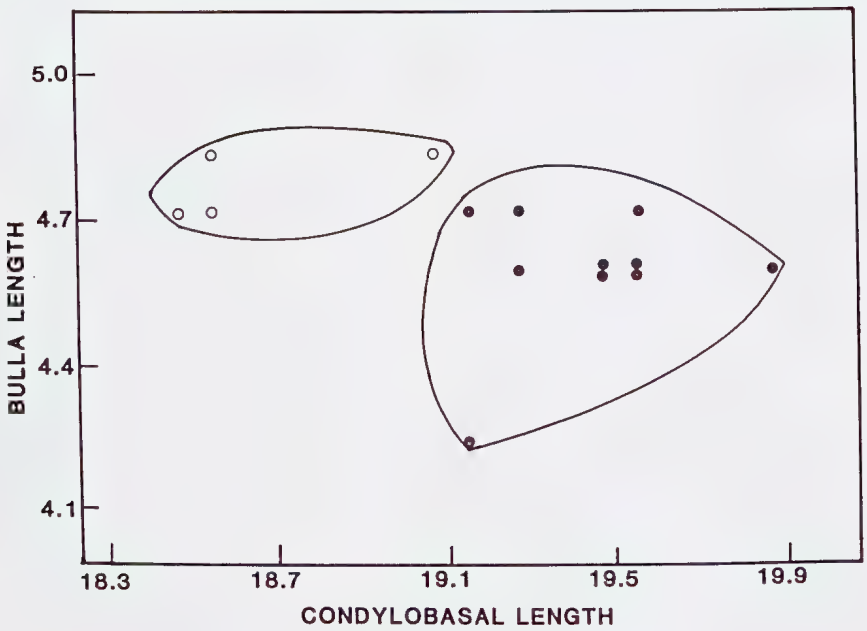

Fig.5. Bivariate plot of bulla length over condylobasal length (in mm) for *Hipposideros corynophyllus* (dot) and *H. edwardshilli* (circle).

along with *H. stenotis* of Australia, clearly form a cluster of closely related species within the *H. cyclops* complex, as all possess very prominent club-like projections on the posterior and intermediate noseleaves. These are either smaller or absent in other members of the *H. cyclops* group in Australasia.

One further record, which may relate to this species, needs discussion. McKean (1968) reports upon a single bat from Aseki, Morobe Province that he refers to *H. semoni*. However, the forearm length (51.8 mm) suggests that this bat was not *H. semoni*, but either *H. corynophyllus* or *H. edwardshilli*. The exact identity of the specimen will probably never be resolved, as it remained in McKean's personal collection until it was destroyed during Cyclone Tracy in 1974 (J. Calaby, personal communication). The record is of potential great importance, however, as it is much further east than other records for these species.

Hipposideros wollastoni Thomas, 1913

Diagnosis. *Hipposideros wollastoni* can be distinguished from all other species of *Hipposideros* in its possession of a posterior accessory noseleaf. This structure is joined to the posterior leaf by two external and two intermediate septa.

Discussion. Examination of the three specimens reported upon by Hill (1985) from Telefomin and Tabubil, 33 obtained by T.F.F. from Telefomin and other localities within a 30 km radius, and a single specimen from the North Coast Range, has revealed considerable variability within this taxon. The Telefomin and North Coast Range samples are sufficiently different to recognise them as distinct subspecies, which are described below. The question as to whether these three taxa should be recognised at the specific or subspecific level is a vexed one. There is little doubt that all three are close relatives, as they are the only *Hipposideros* to possess an accessory posterior noseleaf, an undoubted synapomorphy. The biochemical data, however, suggests that at least *H. w. parnabyi* and *H. w. fasensis* are quite distinct, the data being concordant with recognition at species level. There are also several morphological and colour differences between these taxa. If, however, these two taxa were to be recognised as distinct species at present, problems concerning the nominotypical form would arise. The only known specimen of the nominotypical form cannot be compared with the other taxa biochemically. Furthermore, it is faded and its original colour is uncertain. It can, however, be adequately diagnosed from the other two forms on the basis of its cranium and noseleaf structure. Even if it is accepted, on the basis of biochemistry and morphology, that *H. w. parnabyi* and *H. w. fasensis* are distinct species, it cannot be adequately demonstrated that one or the other is not a subspecies of *H. wollastoni*. To add to the uncertainty, two of the three forms are known from a single specimen. Given these difficulties, it is our decision that, until further data are forthcoming, it is best to regard these as samples representing very distinct subspecies of a single species.

Hipposideros wollastoni wollastoni Thomas, 1913

Table 4

Type material. HOLOTYPE, BMNH 13.6.18.4, adult female in spirit, skull extracted, collected by Dr Wollaston in January 1912 at an elevation of around 750 m at Camp 3 (4°27'S 137°14'E) on the Utakwa River, southern slopes of the Central Cordillera, in what is now Irian Jaya.

Diagnosis. Differing from *H. wollastoni parnabyi* in its shorter ear and cheektooth row length, and lack of a club in the middle of the posterior noseleaf. Differing from *H. wollastoni fasensis* in its shorter forearm and cheektooth row length, broader rostrum, in having the accessory posterior noseleaf shorter than the posterior noseleaf, and in its lesser bizygomatic width.

Discussion. The noseleaf is figured in Hill (1963). No additional material has been reported upon since the discovery of the holotype. The holotype is so badly faded that its original colour cannot be determined, and the colour is not recorded in the type description.

Hipposideros wollastoni parnabyi n.subsp.

Figs 6-10, Table 4

Type material. HOLOTYPE, AM M15892, adult female in spirit, skull extracted, collected from a cave in the Nong River valley adjacent to Miptigin, Telefomin area (5°11'S 141°35'E), 9 July 1985 by T.F. Flannery.

PARATYPES, 32 (see Appendix II).

Etymology. For Harold Edwin Parnaby, in recognition of his contribution to bat taxonomy and conservation.

Diagnosis. Differing from *H. wollastoni wollastoni* in its longer ear (Table 4), greater condylobasal length (Fig.6), possession of a small club in the middle of the posterior noseleaf, and in lacking the fringe of hairs along the posterior margin of the posterior accessory noseleaf (Fig.7). Differing from *H. wollastoni fasensis* n.subsp. in colour, having a brownish (see below) dorsum and Drab Grey venter, as opposed to being black overall; in its longer ear (Fig.8), larger rostral eminences (Table 4, Figs 9,10), in having the accessory noseleaf lower than the posterior noseleaf and in having fewer hairs along the dorsal margin of the accessory posterior noseleaf.

Description. The description of the pelage is taken from a dry skin not discoloured by alcohol (AM

M21745). The flight membranes, noseleaf and ears are close to Sepia (119), but in some specimens (most of which are subadults) the ears can be speckled with pink. The tips of the dorsal fur are close to Hair Brown, but for the basal two thirds the fur is close to Drab-Gray. This underfur shows through in life, giving the animal a pale appearance. The fur of the venter is close to Drab-Gray also, but is several shades lighter than the base of the dorsal fur. This gives the bat a strongly bicoloured appearance, the dorsum appearing darker than the venter. The noseleaf of this subspecies has been described in Hill (1985), and our sample confirms the features noted by him. Hill (1985) describes the differences between the cranium in this subspecies and the nominotypical form. The larger series of skulls now available does not reveal any more significant variability. A statistical summary for the sample is given in Table 4. See Figure 10 for the holotype skull.

Discussion. The Australian Museum holds 33 individuals from the Telefomin, Nong River and Tifalmin areas (see Flannery & Seri, 1990), while the British Museum (Natural History) holds two individuals from Telefomin and one from Tabubil to the South. The town of Tabubil lies at approximately

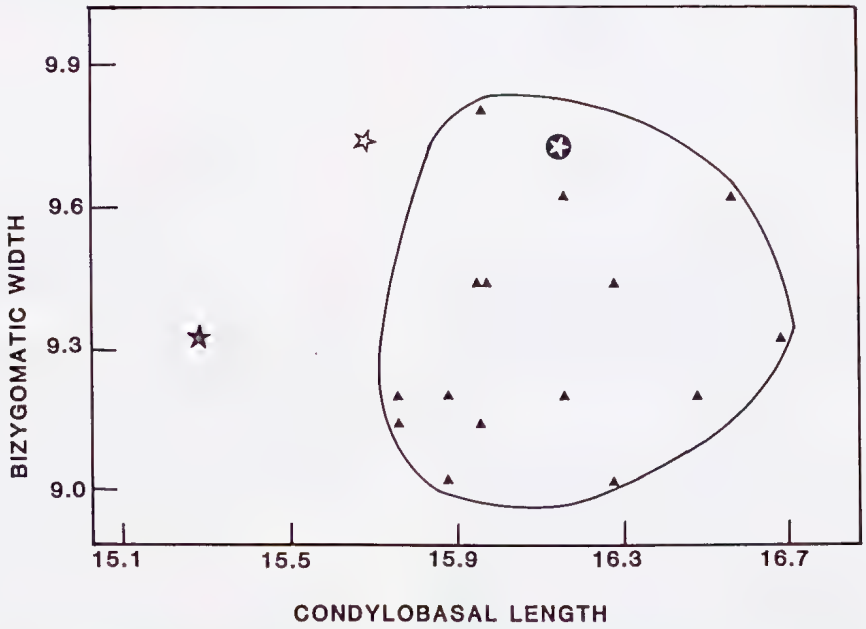

Fig.6. Bivariate plot of bizygomatic width over condylobasal length (in mm) for *H. w. parnabyi* (triangle), *H. w. fasensis* (star in circle), *H. w. wollastoni* (star) and *H. muscinus* (hollow star).

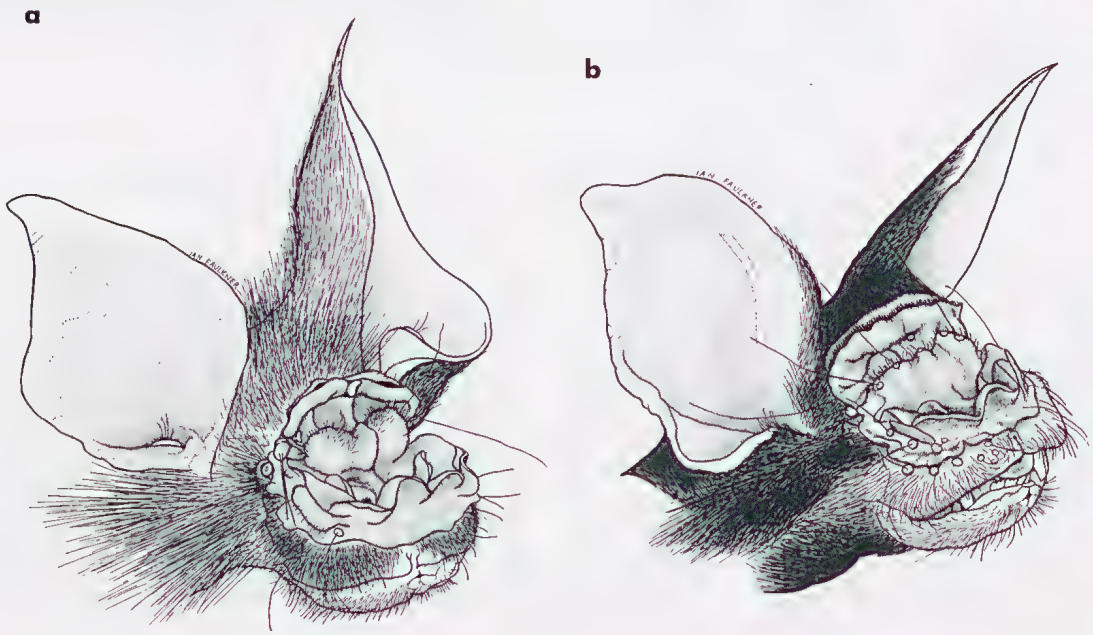

Fig.7. Drawings of the face of a, *H. w. fasensis* and b, *H. w. parnabyi*.

580 m elevation. Vegetational zonation is markedly depressed in the Tabubil area, probably due to near continuous cloud cover and extremely high rainfall. Species typical of forest above 2,000 m elevation in the Telefomin area occur as low as 800 m in the Tabubil area (Flannery & Seri, 1990). This may account for the occurrence of *H. w. parnabyi* at such a low elevation in this region. The Museum of Victoria also holds a single individual (NMV C25494) from Kavorabip (elevation 1500 m) in the Tabubil area. The remaining subspecies of *H. wollastoni* are known from a single specimen each. There is very little morphological variability within the large sample of *H. wollastoni parnabyi* available for study. Juveniles have fur similar in colour to adults, although the ears may have pinkish blotches, and all individuals have a small club-like structure on the posterior noseleaf. There is no sexual dimorphism in size or morphology. All likewise differ from *H. w. fasensis* in having the fringe of hair less well developed on the dorsal margin of the accessory posterior noseleaf. The skulls of 19 individuals (of which 15 are complete adult skulls) have been removed and measured, and they reveal the kind of variability typical of a microchiropteran species that lacks sexual dimorphism.

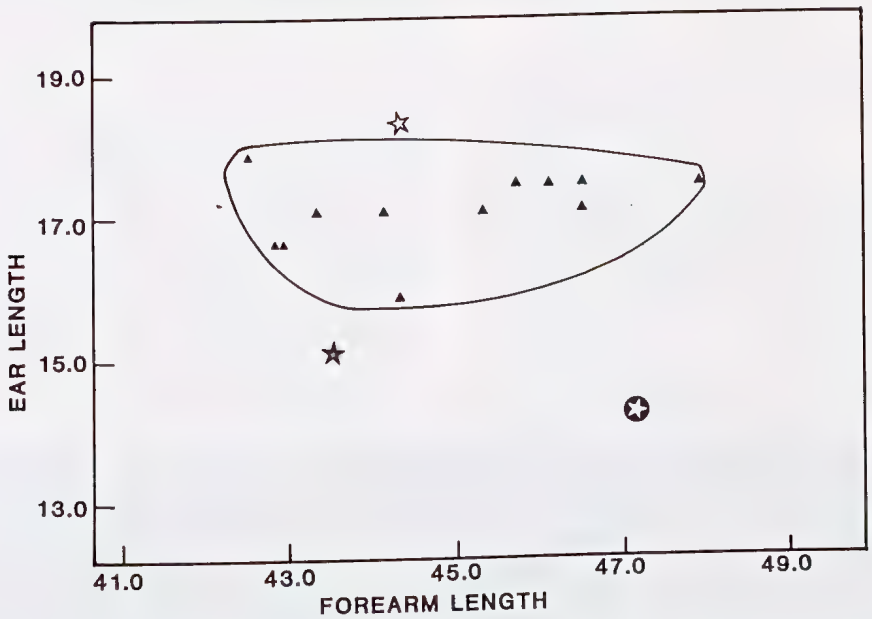

Fig.8. Bivariate plot of ear length over forearm length (in mm) for *H. w. fasensis* (star in circle), *H. w. parnabyi* (triangle), *H. w. wollastoni* (star) and *H. muscinus* (hollow star).

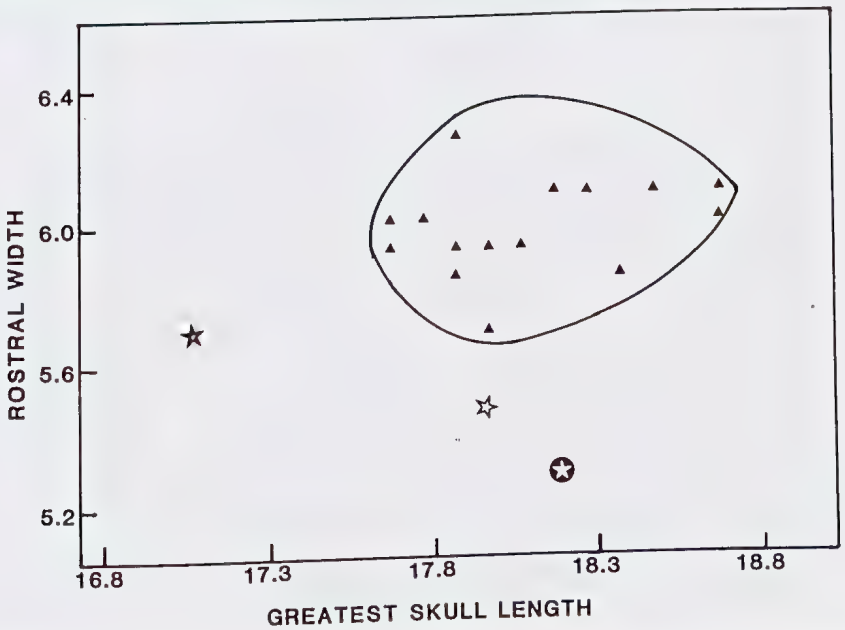

Fig.9. Bivariate plot of rostral width over greatest skull length (in mm) for *H. w. parnabyi* (triangle), *H. w. fasensis* (star in circle), *H. w. wollastoni* (star) and *H. muscinus* (hollow star).

Hipposideros wollastoni fasensis n.subsp.

Figs 6-10, Table 4

Type material. HOLOTYPE, AM M21876, young adult female (basilar suture fused but wing joints still unfused) caught hanging under a small landslip at an elevation of 400-450 m on the hill south of 2Fas Airstrip (3°13'S 141°30'E) West Sepik Province, Papua New Guinea, acquired by T. Flannery, 26 Feb. 1990.

Etymology. After the Fas villages; Sowarnafas (also known as 1Fas), 2Fas and 3Fas. It was due to confusion caused by these names that T.F.F. was stranded in 2Fas Village for a week, when he had planned to work at 3Fas. During this interlude he acquired the holotype of *H. w. fasensis*.

Diagnosis. Differing from *H. wollastoni wollastoni* in its narrow rostral eminences (Fig.9), in that the accessory posterior noseleaf is taller than the posterior noseleaf, the median projection of the intermediate noseleaf is not as pronounced, and the fringe of hairs along the posterior margin of the accessory posterior noseleaf is very well developed (Fig.7a). Differing from *H. wollastoni parnabyi* n.subsp. in being black all over rather than brown and fawn, in having narrow and low rostral eminences, shorter ears (Fig.8a), the accessory posterior noseleaf taller than the posterior noseleaf, in lacking such a prominent median eminence in the centre of the intermediate noseleaf, in lacking a club in the middle of the posterior noseleaf, and in possessing a well-developed fringe of hairs along the posterior margin of the accessory posterior noseleaf (Fig.7a).

Description. The pelage is approximately 5.5 mm long over the midback. Differing from *H. w. parnabyi* in that the dorsum is black, and in that the venter is also black, but with very slight pale tipping. The ears, noseleaf and wing membranes are all black. The left forearm is broken, and the joints of the phalanges of the wings are slightly swollen, which is another indication that the individual was not fully adult. The skin of the noseleaf is black, and the noseleaf differs from that of other *H. wollastoni* in a number of ways. The accessory posterior noseleaf is marginally taller than the posterior noseleaf itself, while in other subspecies the posterior noseleaf is the taller of the two structures (Fig.7). The fringe of hairs along the dorsal margin of the accessory posterior noseleaf is dense, although individual hairs are short. There is no median prominence (club) on the posterior noseleaf (also seen in *H. w. wollastoni*). The median projection of the intermediate noseleaf is small relative to other forms of *H. wollastoni*. The lateral leaflets do not differ (except in colour) from *H. w. parnabyi*.

Fig.10. Photographs of the skulls of a, *Hipposideros wollastoni parnabyi* (AM M15892, holotype) and b, *H. w. fasensis* (AM M21876, holotype).

The rear of the skull is cracked and slightly distorted (which probably happened at the time of capture, see Fig.10). The anterior right moiety of the braincase has a depressed fracture. The skull evidently is from a young adult as the basilar suture is fused, the adult dentition erupted, but the teeth are little worn. The teeth are large relative to condylobasal length (Table 4), which may also indicate that it was not fully grown. In overall shape very similar to *H. w. parnabyi*, but differing in the following: rostral swellings and supraorbital crests not as prominent, the sagittal crest tapers off more rapidly posteriorly. The basicranial region is fractured, and as a result cannot be fully cleaned, dried tissue thus obscures some morphology.

Discussion. The single known specimen of *H. w. fasensis* was caught by a man from Fugere Village near 2Fas Airstrip. There were two bats roosting together under the small overhang left in a bank by a small landslip, one of which escaped. This roost site is very different from that used by *H. w. parnabyi* in the Telefomin area. In several years work, which resulted in the collection of 33 individuals, *H. w. parnabyi* was only encountered at roost in deep, moist limestone caves. Only a single small cave was located in the 2Fas area. It was inhabited by a large colony of *Hipposideros massigtaylorae*.

Although the noseleaf, ear and pelage of *H. w. parnabyi* are distinctive, the skull reveals few differences from other *H. wollastoni*. The teeth are relatively large, and the skull had clearly not reached its full adult size. Forearm length would probably have increased a little by the time growth ceased.

ACKNOWLEDGMENTS. This work was made possible through a distribution from the estate of Miss Winifred Violet Scott. We would like to thank the people of Imonda and 2Fas villages, West Sepik Provinces, for their help and hospitality during our stay. T.F.F. owes a particular debt to councillor John of 2Fas. The staff of the PNG Department of Environment and Conservation deserves our deepest gratitude for making this work possible. Mr Lester Seri of the Nature Conservation Section, along with Mr P. German, are also deeply thanked for their help in the field. Dr Sandra Ingleby kindly commented upon this manuscript, and Dr John Hill made invaluable comments to T.F.F. at the beginning of this project. The colour photographs were taken by Dr H. Cogger and Mr P. German. The black and white photographs were taken by the Australian Museum Photographic Section. Ms Tish Ennis drafted the figures and composited the photographic plates, except for Figure 7 which was drawn by Mr Ian Falkner.

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APPENDIX I

Table 1. Enzymes scored, E.C. Numbers, electrophoretic conditions and inferred genotype for four *Hipposideros* taxa. Enzymes are identified by the abbreviations given in Harris & Hopkinson (1977). Buffer compositions are given in Colgan (1986). Taxa were monomorphic for the stated genotype except that the *H. corynophyllus* (FB96) was heterozygous for a variant G-6-PDH allozyme. Genotypes have been inferred on the supposition that the loci are not sex-linked.

Enzyme	E.C. No.	Buffer	Locus	Inferred Genotypes			
				H. wollastoni parnabyi	*H. wollastoni fasensis*	*H. edwardshilli*	*H. corynophyllus*
AAT	2.6.1.1	TC 100	1	11	11	11	11
			2	11	11	11	11
AK	2.7.4.3	TC 100	1	22	11	22	22
			2	11	11	11	11
ALD	4.1.2.13	TEM 50	1	11	11	11	11
ENOL	4.2.1.11	TEM 50	1	11	11	22	22
EST	3.1.1.1	TEM 50	1	11	11	22	22
FDP	3.1.3.11	TEM 50	1	11	11	33	22
FH	4.2.1.1	TC 100	1	11	11	11	11
GA-3-PDH	1.2.1.12	TEM 50	1	11	11	11	11
GPD	1.1.1.8	TEM 50	1	11	11	11	11
			2	11	11	11	11
General Protein		TEM 50	1	22	22	11	11
			2	22	22	11	11
			3	11	11	11	11
G-6-PDH	1.1.1.49	TEM 50	1	11	11	22	22
			2	22	11, 12	null	null
GPI	5.3.1.9	TEM 50	1	11	11	22	11
IDH	1.1.1.42	TEM 50	1	33	33	11	12
			2	11	11	11	11
LDH	1.1.1.27	TC 100	1	22	22	33	11
			2	11	11	11	11
MDH	1.1.1.37	TEM 50	1	11	11	11	11
			2	11	11	11	11
MPI	5.3.1.8	TEM 50	1	22	11	22	22
			2	11	11	null	null
6-PGDH	1.1.1.44	TEM 50	1	33	11	22	22
PGM	2.7.5.1	TEM 50	1	22	22	22	12
SDH	1.1.1.14	TEM 50	1	22	22	11	11
SOD	1.15.1.1	TEM 50	1	11	11	22	22
			2	11	11	null	null
TPI	5.3.1.1	TEM 50	1	11	11	11	11
			2	11	11	11	11
UDPG	2.7.7.9	TC 100	1	11	11	33	22

Table 2. Genetic distances between four *Hipposideros* taxa. The figures below the diagonal refer to Wright's modification of Rogers' distance and those above to Nei's standard distance. Distances are based only on those loci which are represented in both members of the relevant pair.

Taxon	*H. e.*	*H. c.*	*H. w. p.*	*H. w. f.*
H. edwardshilli	–	0.115	0.544	0.500
H. corynophyllus	0.330	–	0.661	0.614
H. wollastoni parnabyi	0.648	0.696	–	0.159
H. wollastoni fasensis	0.622	0.672	0.381	–

Table 3. Summary of measurements for *Hipposideros edwardshilli*, *H. corynophyllus*, *H. stenotis* and *H. semoni*. Measurements are as follows: 1) forearm length, 2) tail length, 3) ear length, 4) condylobasal length, 5) greatest skull length, 6) bizygomatic breadth, 7) width across rostral swellings, 8) bimastoid breadth, 9) C^1-M^3 length (alveolar), 10) M^2-M^2 breadth (alveolar, external), 11) bulla width.

	Variable	Mean	S.D.	N	Median	Minimum	Maximum
H. edwardshilli	1	50.25	.66	4	50.20	49.60	51.00
	2	13.57	1.80	4	14.10	11.10	15.00
	3	20.45	1.00	4	20.60	19.30	21.30
	4	18.60	.27	4	18.50	18.40	19.00
	5	21.02	.29	4	21.00	20.70	21.40
	6	11.07	.19	4	11.15	10.80	11.20
	7	6.95	.06	4	6.95	6.90	7.00
	8	10.07	.05	4	10.10	10.00	10.10
	9	7.93	.09	4	7.95	7.80	8.00
	10	8.00	.08	4	8.00	7.90	8.10
	11	4.75	.06	4	4.75	4.70	4.80
H. corynophyllus	1	53.03	.81	10	52.80	52.00	54.60
	2	10.58	1.06	10	10.85	9.00	12.00
	3	20.67	1.13	11	20.50	18.90	22.60
	4	19.35	.22	11	19.40	19.10	19.80
	5	21.88	.75	11	21.90	19.80	22.60
	6	11.45	.18	11	11.50	11.10	11.60
	7	6.68	.23	11	6.70	6.40	7.00
	8	10.26	.14	11	10.30	10.00	10.50
	9	8.30	.11	11	8.30	8.10	8.40
	10	8.21	.17	10	8.15	8.10	8.60
	11	4.59	.15	10	4.60	4.20	4.70
H. stenotis	1	45.00	1.00	3	45.00	44.00	46.00
	2	26.67	.58	3	27.00	26.00	27.00
	3	20.00	1.00	3	20.00	19.00	21.00
	4	17.05	.57	4	16.80	16.70	17.90
	5	18.95	.81	4	19.05	17.90	19.80
	6	10.67	.30	4	10.70	10.30	11.00
	7	6.03	.36	4	6.15	5.50	6.30
	8	8.38	.43	4	8.50	7.80	8.70
	9	7.05	.33	4	6.95	6.80	7.50
	10	7.30	.28	4	7.20	7.10	7.70
	11	4.05	.37	4	4.10	3.60	4.40
H. semoni	1	40.53	2.20	3	41.50	38.00	42.10
	2	25.00	4.20	2	25.00	22.00	28.00
	3	19.23	1.10	3	19.70	18.00	20.00
	4	15.25	.79	4	15.05	14.60	16.30
	5	17.05	.79	4	17.05	16.20	17.90
	6	9.35	.26	4	9.30	9.10	9.70
	7	5.65	.38	4	5.50	5.40	6.20
	8	7.30	.56	4	7.20	6.80	8.00
	9	5.83	.31	4	5.90	5.40	6.10
	10	6.30	.27	4	6.40	5.90	6.50
	11	3.50	.22	4	3.45	3.30	3.80

Table 4. Summary of measurements for the three subspecies of *Hipposideros wollastoni* and *H. muscinus*. See Table 3 for explanation of measurements.

	Variable	Mean	S.D.	N	Minimum	Maximum
H. w. fasensis	1	46.80	–	1	–	–
	2	23.60	–	1	–	–
	3	14.30	–	1	–	–
	4	16.10	–	1	–	–
	5	18.10	–	1	–	–
	6	9.70	–	1	–	–
	7	5.30	–	1	–	–
	8	7.80	–	1	–	–
	9	6.90	–	1	–	–
	10	6.50	–	1	–	–
	11	3.80	–	1	–	–
H. w. parnabyi	1	44.67	1.70	15	42.30	47.50
	2	25.27	1.60	12	23.00	28.00
	3	17.06	.49	12	15.90	17.70
	4	16.05	.29	15	15.70	16.60
	5	18.02	.33	15	17.60	18.60
	6	9.30	.23	15	9.00	9.80
	7	5.97	.14	15	5.70	6.20
	8	7.75	.42	15	7.10	8.40
	9	6.67	.15	15	6.50	7.00
	10	6.66	.18	13	6.20	6.90
	11	3.77	.11	13	3.60	4.00
H. w. wollastoni	1	43.20	–	1	–	–
	2	27.00	–	1	–	–
	3	15.00	–	1	–	–
	4	15.20	–	1	–	–
	5	17.00	–	1	–	–
	6	9.30	–	1	–	–
	7	5.70	–	1	–	–
	8	8.00	–	1	–	–
	9	6.40	–	1	–	–
	10	6.80	–	1	–	–
	11	–	–	-	–	–
H. muscinus	1	44.00	–	1	–	–
	2	28.00	–	1	–	–
	3	18.00	–	1	–	–
	4	15.60	–	1	–	–
	5	17.90	–	1	–	–
	6	9.70	–	1	–	–
	7	5.40	–	1	–	–
	8	8.00	–	1	–	–
	9	6.50	–	1	–	–
	10	6.70	–	1	–	–
	11	3.70	–	1	–	–

APPENDIX II

Specimens examined in Australia for this analysis, excluding type specimens (see text). Specimens marked with an asterisk were used in the metric analysis.

Hipposideros corynophyllus – AM M15889*, 17889, 17890*, 17971, 17972*, 17973, 17974, 17975, 17976, 17977, 17978*, 17979, 17980, 17981, 17982*, 17983*, 17984*, 17985, 17986*, 17987, 17988*, 17989*, 19985, 21742*, all Telefomin and Tifalmin areas, West Sepik Province, PNG.

Hipposideros wollastoni parnabyi – AM M15885*, 15886*, 15887, 15888*, 15890*, 15891*, 15892*, 15893*, 15894*, 15895*, 15896*, 15897*, 16721, 17917, 17918, 17919*, 17920, 17921, 17922, 17923, 17924, 17925*, 17926*, 17927, 17928, 17929*, 17930, 17931*, 21743*, 21744*, 21745*, 21875, 23203, all Telefomin and Tifalmin areas, West Sepik Province, PNG.

Hipposideros muscinus – AM M17331* near Noru Village, Chimbu Province, PNG.

Hipposideros semoni – AM M16614*, 16616* Iron Range, Qld, 17330* Varirata National Park, Central Province, PNG, WAM18055* Helenvale, Qld

Hipposideros stenotis – CM10020* Pine Creek, NT, WAM10471* Bonaparte Archipelago, WA, 19391* Koolan Island, WA, 19893* no locality.

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Revision of the Genus *Melonycteris* (Pteropodidae: Mammalia)

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ABSTRACT. The genus *Melonycteris* consists of three species: *M. melanops* Dobson, 1877, *M. woodfordi* (Thomas, 1887), and *M. fardoulisi* n.sp. *Melonycteris melanops* is monotypic and widespread in the Bismarck Archipelago. It is orange in colour, and is unique in the genus in retaining a claw on digit two of the wing and in having P^1 and M_3 reduced. *Melonycteris woodfordi* is an orange-coloured species also, which is found in the northern and eastern Solomon Islands, and consists of two subspecies (the smaller *M. w. woodfordi*, found on the islands from Buka to Ysabel, and the larger *M. w. aurantius* on the Nggela Group). *Melonycteris w. aurantius* is unique in the genus in that females are usually larger than males, while in *M. w. woodfordi* the sexes are similar in size. *Melonycteris fardoulisi* n.sp. is a predominantly brownish species in which the sexes differ in colour and where males are markedly larger than females. It is distributed in the western and southern islands of the main Solomons chain, and includes four subspecies (*M. f. fardoulisi* n.subsp. from Makira, *M. f. maccoyi* n.subsp. from Malaita, *M. f. schouteni* n.subsp. from Guadalcanal and *M. f. mengermani* n.subsp. from Western Province). The subspecies differ in size, colour and degree of sexual dimorphism.

FLANNERY, T.F., 1993. Revision of the genus *Melonycteris* (Pteropodidae: Mammalia). Records of the Australian Museum 45(1): 59–80.

Species of the genus *Melonycteris* are endemic to the Bismarck Archipelago and Solomon Islands, Melanesia. They are brightly-coloured bats, often having profuse pink spotting on their black wing membranes. The dorsal fur can be bright orange, and white 'epaulettes' may be present. They are members of the subfamily Macroglossinae and are nectar feeders, Kress (1985) demonstrating that on Guadalcanal at least the blossoms of *Heliconia solomonensis* are visited. The first of these distinct bats to be described was *Melonycteris melanops* Dobson, 1877 (syn. *Pteropus (Cheiropteruges) alboscapulatus* Ramsay, 1877). This species is now known to occur on many islands of the Bismarck Archipelago (Fig.1). In 1887 Thomas described a new genus and species, *Nesonycteris woodfordi*, from Alu Island (the type locality) and nearby Fauro Island in the Shortland Group, northern Solomons. Pohle (1953) recognised the close similarity between species of *Nesonycteris* and *Melonycteris*, and suggested that *Nesonycteris* should be placed in synonymy with *Melonycteris*, the older and thus correct generic name. All subsequent workers have accepted this synonymy.

A third species of *Melonycteris*, *M. aurantius* was

described by Phillips (1966), based upon one adult female (the holotype) from Florida Island in the Nggela Group and five subadult female paratypes from Choiseul, Solomon Islands. Phillips suggested that *M. woodfordi* and *M. aurantius* occurred in sympatry as both species were supposedly taken in the same net on Choiseul. Phillips (1968) listed four specimens of *Melonycteris woodfordi* which were also supposedly from Choiseul.

The only other primary literature records for species of *Melonycteris* are those of McKean (1972) who described nine specimens of *M. woodfordi* from various locations on Bougainville; Sanborn (1931) who notes a specimen from the Russell Islands; and Smith & Hood (1981), who mention that *M. melanops* was localised but relatively abundant in their study areas on New Britain and New Ireland. They mention the capture of 13 individuals in a single net at one locality.

This research is based primarily upon material collected by myself and others in the Bismarck Archipelago and the Solomon Islands during 1987-1991. The Australian Museum now holds 129 specimens of *Melonycteris*, most of which were collected during this period. Examination of this material revealed that existing taxonomic concepts are incorrect, and that both taxonomic diversity was greater, and zoogeographic patterns quite different, from that previously described.

Materials and Methods

In addition to the holdings of the Australian Museum I borrowed extensively from the collections of the Bishop Museum and the Australian Nation Wildlife Collection during the course of this study. During an overseas study tour in 1989 I also examined all *Melonycteris* specimens available in the American Museum of Natural History; Bishop Museum; British Museum (Natural History); and Los Angeles County Museum. Thus most, if not all, world museum holdings of *Melonycteris* were examined.

All of the AM M specimens collected during the 1987, 1990 and 1991 expeditions to the Solomon Islands were captured in mistnets. Despite considerable efforts neither hunting nor searching by local people were successful in obtaining *Melonycteris* specimens.

Measurements throughout are given in millimetres and weights in grams. Specimen number prefixes are as follows AM – Australian Museum; AMNH – American Museum of Natural History; BM – Bishop Museum; BMNH – Natural History Museum (London); CM – National Wildlife Collection (Canberra); LACM – Los Angeles County Museum. Specimens used in the morphometric analysis are marked with an asterisk. Colours where capitalised follow Smithe (1974). The STATISTIX package was used for statistical analysis, and results of 't' tests were considered significant at the level given assuming unequal variances unless otherwise stated. Primary data will be supplied upon request to the

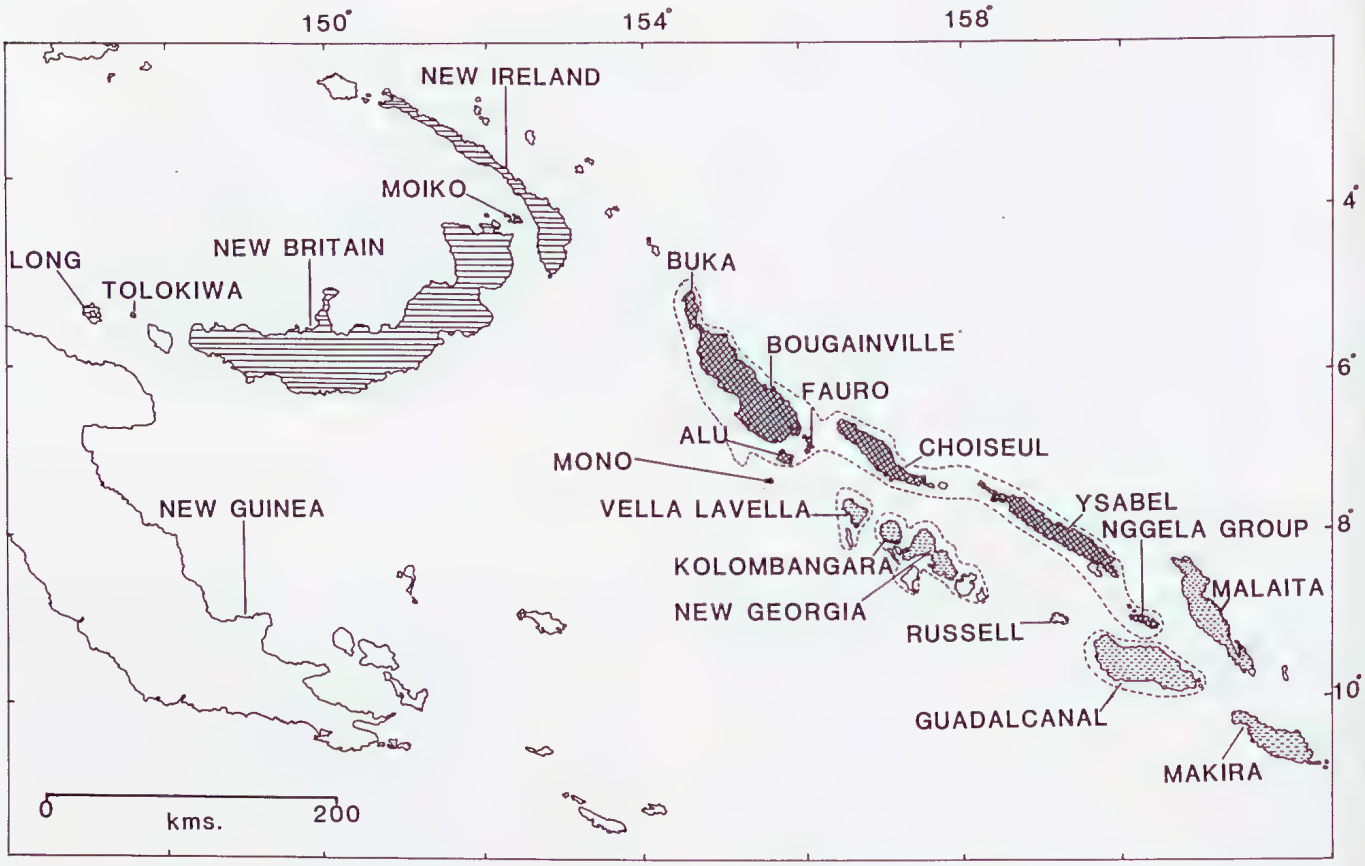

Fig.1. The distribution of the species of *Melonycteris*, including localities mentioned in the text. Horizontal bar = *M. melanops*, hatching = *M. woodfordi*, spotting = *M. fardoulisi*.

author.

Tables 1-5 are included in the Appendix.

Systematics

Pteropodidae

Macroglossinae

Melonycteris Dobson, 1877

Melonycteris melanops Dobson, 1877

Figs 2,4, Table 1

Type material. HOLOTYPE, BM 77.7.18.10, skin and skull of an adult male collected on New Ireland by the Rev. G. Brown.

Synonym. *Pteropus* (*Chiropteruges*) *alboscapulatus* Ramsay, 1877. Holotype AM P1271* (Palmer register), adult male skin with skull inside. The locality given by Ramsay (in the title of the paper only) is Duke of York Island. A label accompanying the specimen marked as the holotype reads as follows "Loc. New Ireland, Bismarck Archipelago. Hab. Duke of York and New Ireland, Bismarck Arch." The specimen was collected by the Rev. George Brown. The specimen marked as the holotype matches in colour and measurements the specimen described by Ramsay.

Other specimens examined. New Ireland; AM M19638*, AM M19933*, AM M20061*, AM M20114*, LACM67048, LACM67054, LACM67062, LACM67065. New Britain; AM M20063*, AM M20064*, AM M20163, AM M201644*, LACM65777. Locality unknown AM M2417*. Long Island AMNH 237311, Tolokiwa Island AMNH 237312.

Diagnosis. *Melonycteris melanops* can be distinguished from other species of *Melonycteris* in possessing the following features: shoulders with white epaulettes; base of fur black, and venter darker; digit 2 of wing clawed; P^1 rudimentary, M_3 is greatly reduced in size (Fig.4).

It further differs from *M. fardoulisi* in that the dorsum is more rufescent, and the sexual dimorphism in the canine and sagittal crest is not as great. It differs further from *M. woodfordi* in that males usually possess a larger sagittal crest.

Distribution. Confined to the Bismarck Archipelago, where it has been recorded from the islands of New Ireland, New Britain, Long, Tolokiwa, and Moiko (in the Duke of Yorks, and possibly other islands in that group). Recent surveys of Manus Island and northern New Guinea by the author have confirmed the absence of this species and indeed any other members of the genus at these localities.

Discussion. Although only small numbers are available, it appears that there is little morphological variation between the New Britain, Duke of York and New Ireland samples of *M. melanops*. Some specimens from New Ireland have a less brilliant orange dorsum and a smaller white epaulette than New Britain animals, but populations from the two islands do not differ consistently in these or other features. Table 1 indicates that New Ireland animals may be slightly smaller in interorbital and postorbital width, but larger in C^1-M^2 length. These differences however may simply reflect age differences and small sample size (the postorbital width at least decreases with age in *M. woodfordi*, the only species for

Type of Cheiropterugas alboscapulatus, Ramsay.]
1271.
FRUIT BAT.
MELONYCTERIS MELANOPS, Dobson.
Loc. NEW IRELAND, BISMARCK ARCHIPELAGO.
Hab. DUKE OF YORK I. & NEW IRELAND, BISMARCK ARCH.

Fig.2. Holotype (AM P1271) of *Cheiropteruges alboscapulatus* Ramsay.

which large samples are available, see below). The single specimen examined from Tolokiwa Island is small in condylobasal length and bizygomatic width relative to animals from elsewhere. However, it is typical of the species in its pelage and morphology. The single skin without skull from Long Island is also typical in colour for the species. Further samples are necessary to determine if the metric differences discussed here are typical for the various island populations. However, the differences appear slight and do not seem to warrant taxonomic recognition.

I have found *Melonycteris melanops* to be uncommon both on New Ireland and New Britain, with a total of only eight specimens being taken during extensive mammal surveys of both islands. Smith & Hood's (1981) observations, however, suggest that the species can sometimes be locally abundant.

Melonycteris woodfordi (Thomas, 1887)

Figs 3,6-8, Table 2

Type material. HOLOTYPE, BM 87.1.18.9*, adult male skin and skull collected at Alu, Shortland Islands by C.M. Woodford.

Diagnosis. *Melonycteris woodfordi* differs from *M. melanops* in possessing larger P^1 and M_3 and in lacking white epaulettes, black underfur, and a claw on digit 2. It differs from *M. fardoulisi* n.sp. in being orange rather than brownish dorsally and having no difference in colour between the sexes, sagittal crest less well developed in adult males (except for some *M. w. aurantius*), males not significantly larger than females (at P less than 0.10) in condylobasal length and cheektooth length, and sexual dimorphism in bizygomatic width, canine length, and canine morphology less pronounced (Tables 2-4, Fig.3).

Discussion. *Melonycteris woodfordi* is known from many islands in the northern part of the Solomon Island chain, and is presumably widespread throughout that region. It has been recorded from the islands of Buka, Bougainville, Mono, Oblari, Alu, Fauro, Choiseul, Ysabel, Russel, Nggela and Florida. (Fig.1). Within this distribution two distinct subspecies can be distinguished: *M. w. woodfordi* of Buka, Bougainville, Mono, Alu, Fauro, Choiseul, and Ysabel; and *M. w. aurantius* from Nggela and Florida.

Melonycteris woodfordi woodfordi (Thomas, 1887)

Figs 3-5, Table 3

Other specimens examined. Buka: AM M19816*.

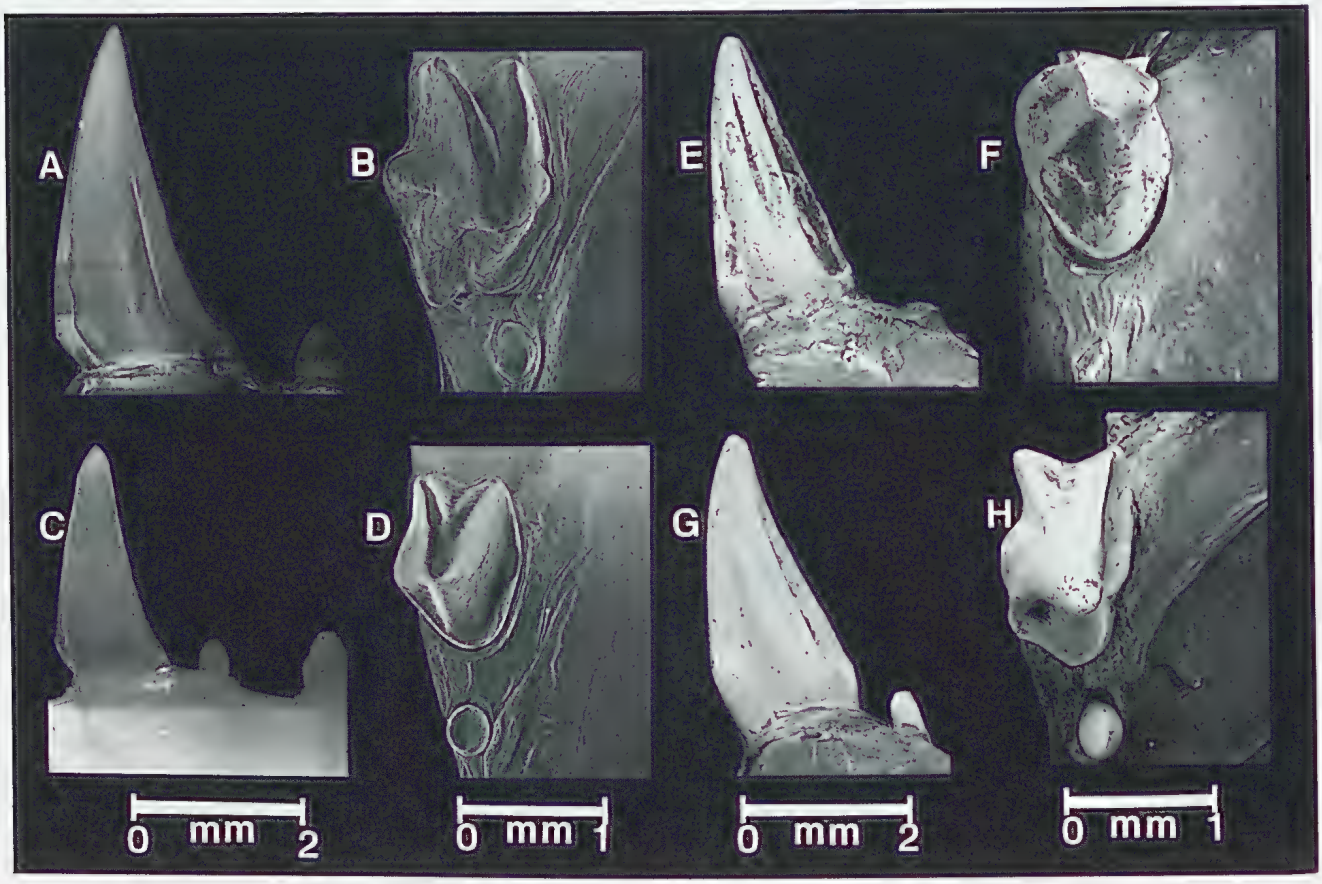

Fig.3. The canines of *Melonycteris fardoulisi fardoulisi*: A, B – AM M18833 male, and C, D – AM M18849 female. Canines of *Melonycteris woodfordi woodfordi*: E, F – AM M6576 male, G, H – AM M6298 female.

Bougainville: AM M6289*, AM M6532, AM M6576*, AM M6577, AM M6653, AM M6654, AM M6655, AM M6656; CM583*, CM584*, CM585*, CM586*, CM587*, CM588*, CM589, CM590*, CM591*; BM22357, BM61083, BM61085, BM61087*, BM61105, BM61167*, BM61160*, BM61276*, BM61303*. Mono: AM M23185, AM M23816, AM M23787, AM M23788, AM M23790*, AM M23791*, AM M23792, AM M23793, AM M23809*, AM M23810*, AM M23811*, AM M23812*, AM M23815*, AM M23816*, AM M24194, AM M24195, AM M24196, AM M24197, AM M24198, AM

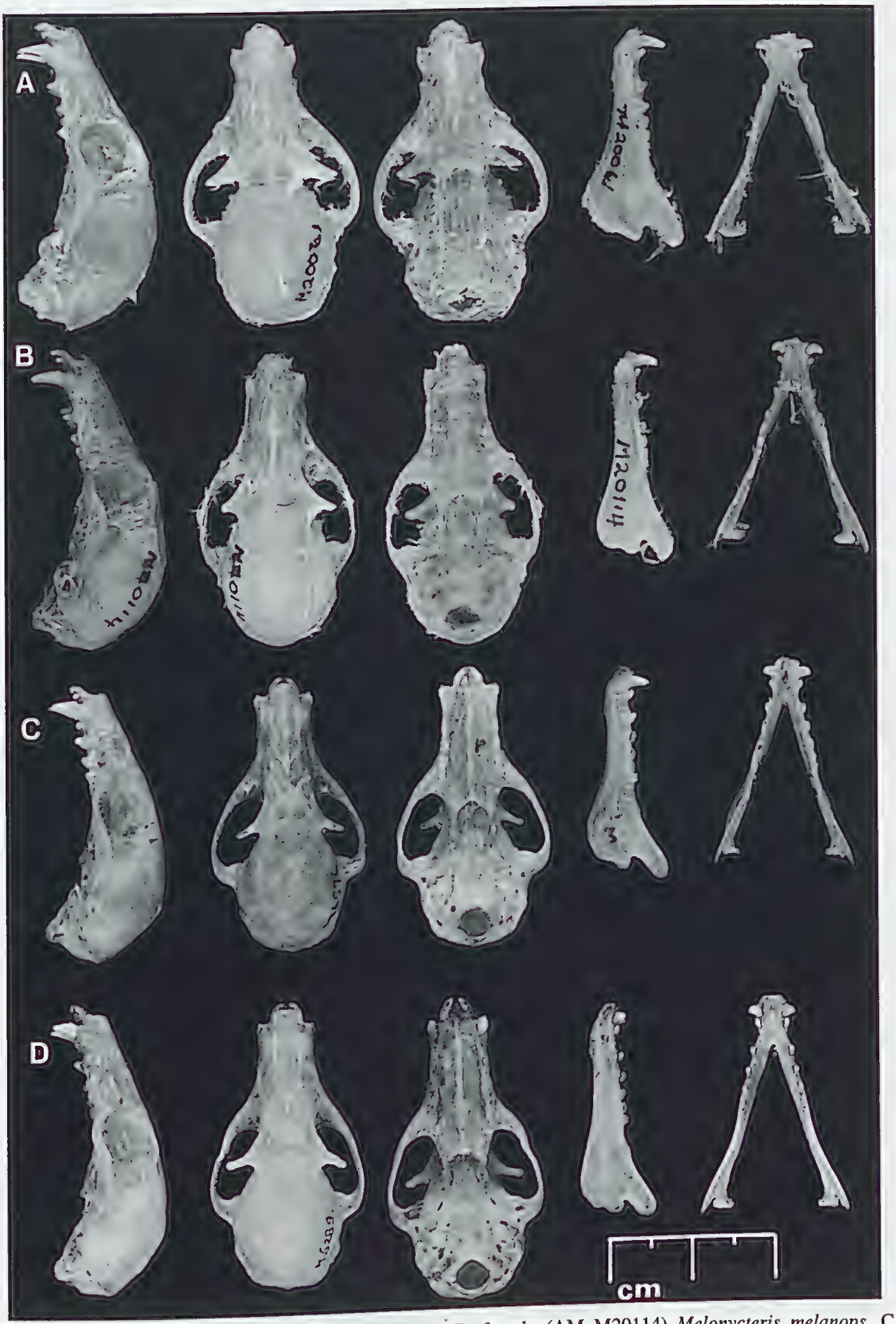

Fig.4. A, the cranium of a male (AM M20061), and B, female (AM M20114) *Melonycteris melanops*, C, cranium of a male (AM M6576), and D, female (AM M6289) *Melonycteris woodfordi woodfordi*.

M24199, AM M24200, AM M24201, AM M24202, AM M24203, AM M24204, AM M24205, AM M24026, AM M24027, AM M24028, AM M24029, AM M24210, AM M24211, AM M24212, AM M24213, AM M24214, AM M24215, AM M25055, AM M25216. Oblari Island (Shortlands): AM M23784, AM M23785*, AM M23786*, AM M23789*, Choiseul: AM M18828*, AM M18829*, AM M18844*, AM M18845*, AM M18846*, AM M21807*, AM M21808*, AM M21809*, AMNH 99916; BM23615, BM23617, BM23558, BM23681, BM23694. Ysabel: AM M18837*, AM M18838*, AM M18839, AM M18840, AM M18842*, AM M18847*, AM M18868, AM M21810, AM M21811, AM M23794* AM M23813*; AM M24216, AM M24217, AM M24218, AM M24219, BM24255*

Diagnosis. *Melonycteris w. woodfordi* differs from *M. w. aurantius* in being significantly smaller (P less than 0.10) in all parameters measured except upper cheektooth row length and upper canine length in males, and postorbital width in females. It further differs in lacking a sagittal crest in males, and in that females are not significantly larger (P less than 0.10) than males in condylobasal length, postorbital width and cheektooth row length.

Distribution. This subspecies has been recorded from the islands of Buka, Bougainville, Alu, Fauro, Mono, Oblari, Choiseul and Ysabel (Fig.1).

Discussion. There is some slight variation in size between populations of *M. w. woodfordi*. Individuals from the Shortlands tend to be the largest as reflected by forearm length (Fig.5), while those from Choiseul are smallest. This pattern is rather curious, as the Shortlands and Choiseul are separated by less than 40 km, and the majority of the Shortland Islands were joined with Choiseul during periods of lowered sea level in the late Pleistocene. Despite these differences there are extensive overlaps in size between various island populations, and no important morphological differences exist between samples from the various islands. Colour varies only slightly between individuals. The most sombre orange individuals tend to be from the Shortlands, while some individuals from Choiseul are the brightest, including the specimens that Phillips (1966) designated paratypes of *M. aurantius*. These specimens, however, are clearly subadult *M. woodfordi* and conform closely in morphology, size and colour with the Australian Museum sample from Choiseul (see below).

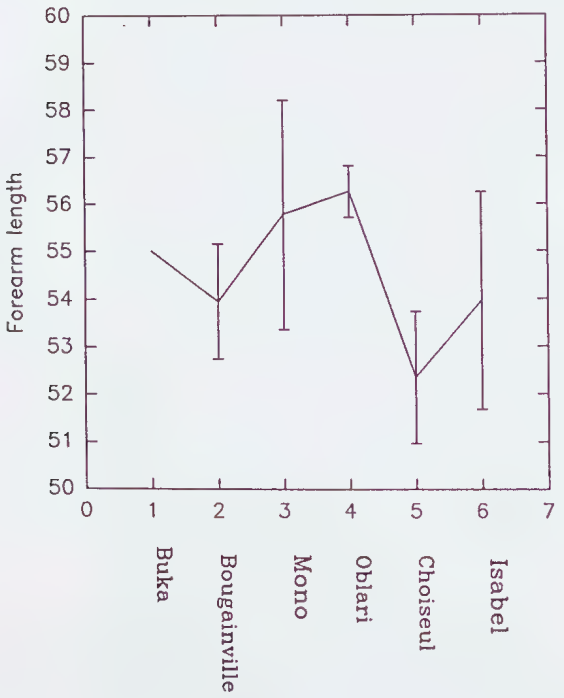

Fig.5. A, forearm length (mean and 95% confidence limits) of adults of various populations of *Melonycteris woodfordi woodfordi*.

Melonycteris woodfordi woodfordi shows the least sexual dimorphism of any of the forms of *Melonycteris*. The only statistically significant differences between the sexes (P less than 0.10) are bizygomatic width and canine length (Table 2, Fig.6). Both are however highly significant differences (P less than 0.0010). There are also some non-metric differences in cranial morphology between the sexes. In females the lines of insertion of the temporals remains widely separated over most of the calvarium. They gradually converge posteriorly and may meet near the occipital crest. Although there is never a sagittal crest in males, the lines of insertion of the temporals converge and join in about the middle of the calvarium. This suggests that temporal muscle mass is greater in males, which is probably related to the greater width of the zygomatic arches and generally larger canines in males.

The locality given by Phillips (1968) for his *M. woodfordi* sample is incorrect. He reported that all four specimens were from Choiseul. In fact, BM 23413, BM 23414, and BM 23434 are from Kolombangara Island, while BM 23275 is from Vella Lavella Island, both in Western Province. These specimens are all assigned here to a new species (see below).

I have had no experience of this subspecies in the field, although judging from museum records it can be locally abundant. It has been captured in some numbers in coconut plantations on Ysabel and Choiseul. Although most records of *M. w. woodfordi* are from near sea level there is a series in the Bishop Museum from Mutahi Village, 18 km south-west of Tinputz, Bougainville, that come from an altitude of 700 m. They are indistinguishable in morphology from individuals from lower altitudes and represent the highest altitudinal record for this taxon.

Melonycteris woodfordi aurantius Phillips, 1966

Figs 7,8, Table 2

Type material. HOLOTYPE, BM24440*, adult female skin and skull, collected at Haleta, Florida Island (9°07'S 160°27'E), Nggela Group, Solomon Islands, 11 Oct. 1964, P.J. Shanahan.

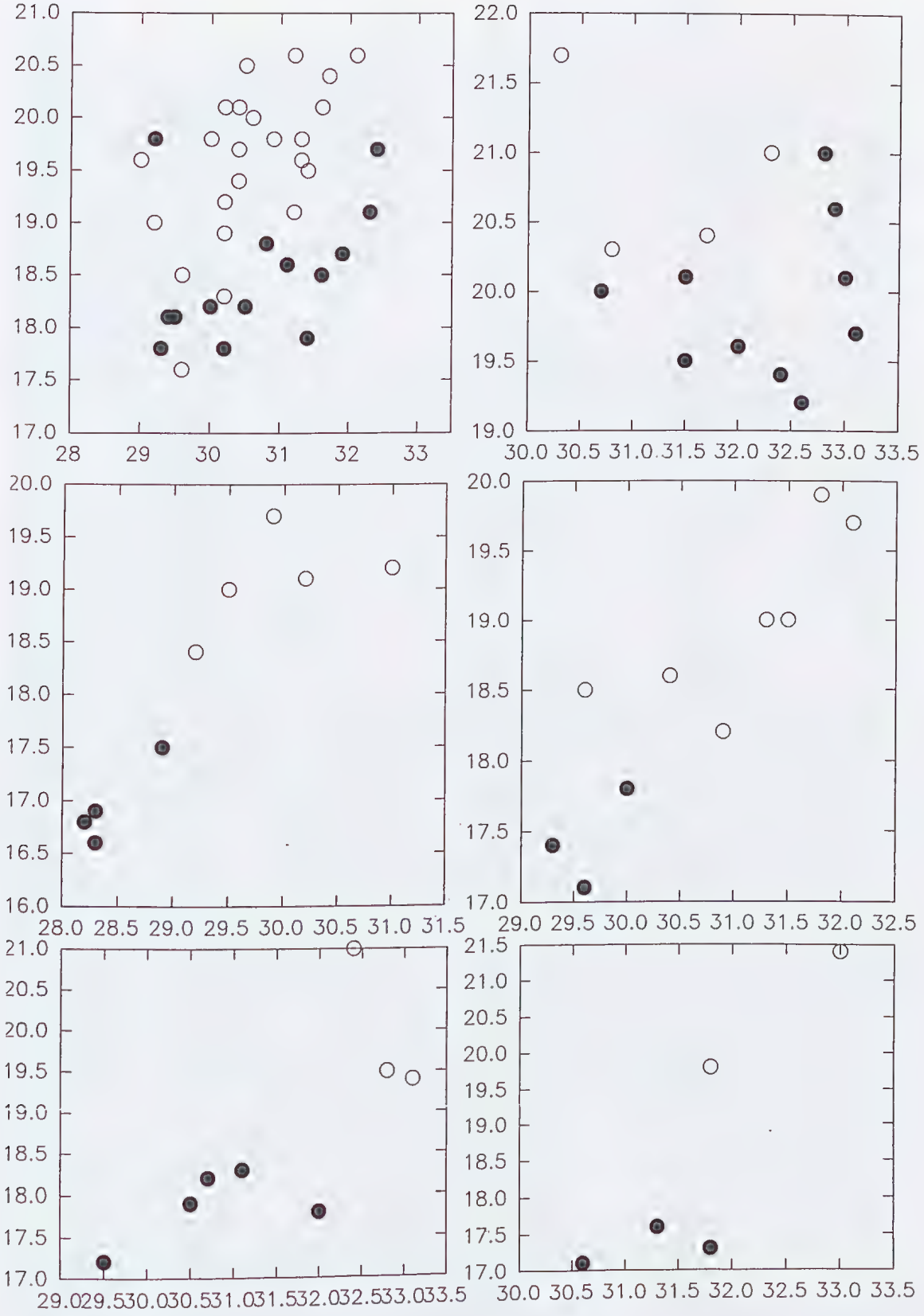

Fig.6. Bivariate plot of bizygomatic width (vertical axis) over condylobasal length (horizontal axis) for adult males and females of the Solomon Islands subspecies of *Melonycteris*. From upper left to lower right, *Melonycteris woodfordi woodfordi*, *M. w. aurantius*, *M. fardoulisi mengermani*, *M. f. schouteni*, *M. f. maccoyi*, *M. f. fardoulisi*.

Other specimens examined. Nggela: AM M18832*, AM M18835*, AM M18843*, AM M18869, AM M24044, AM M24047*, AM M24048*, AM M24049*, AM M24050*, AM M24051*, AM M24052*, AM M24053*, AM M24054*, AM M24055*, AM M24056*, AM M25023, AM M25024, AM M25025, AM M25026, AM M25027, AM M25028, AM M25029, AM M25030, AM M25031, AM M25032, AM M25033, AM M25034, AM M25035, AM M25037, AM

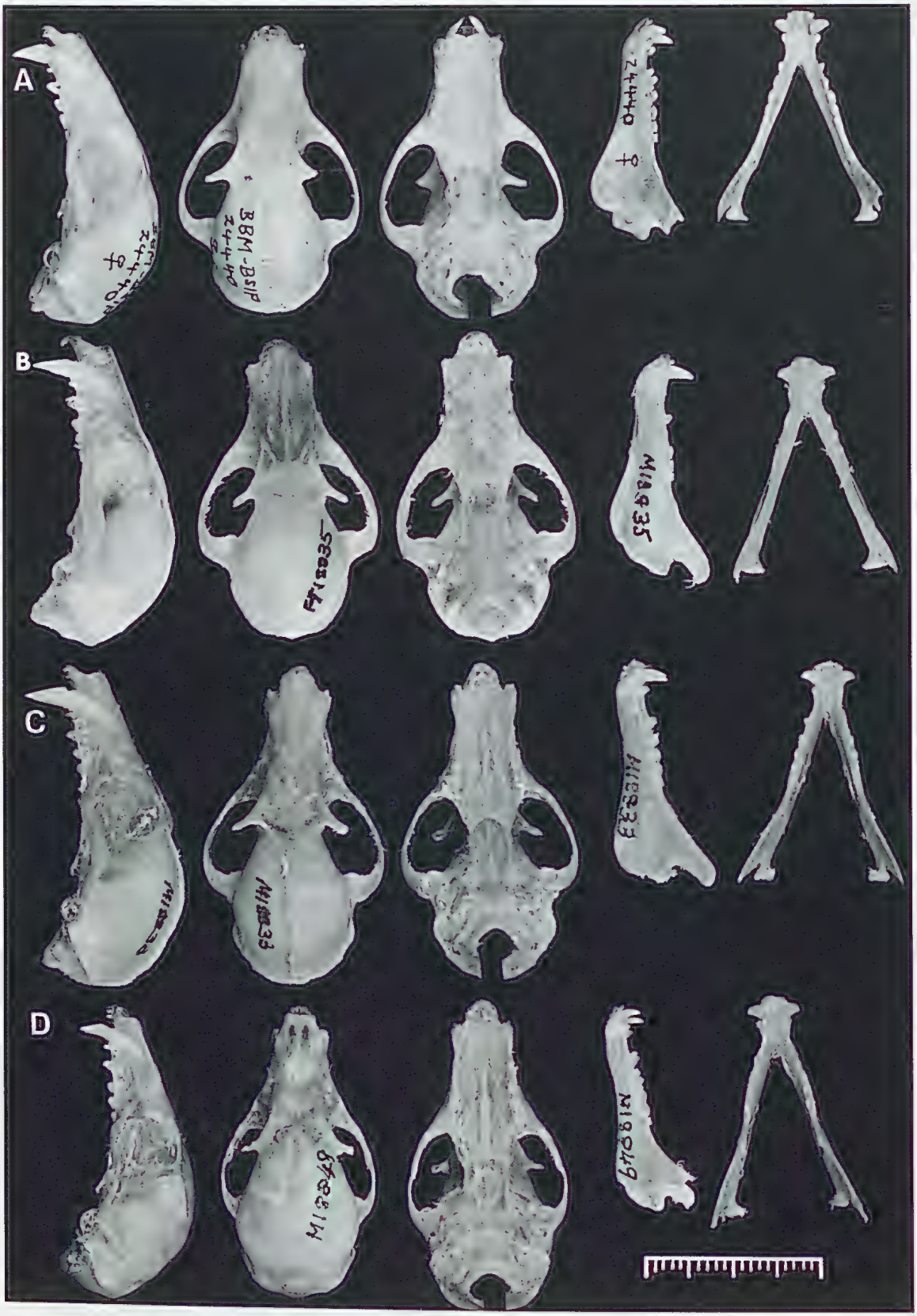

Fig.7. A, cranium of the holotype of *Melonycteris woodfordi aurantius* (BM24440, female); B, cranium of male *M. w. aurantius* (AM M18835); C, cranium of holotype male *Melonycteris fardoulisi fardoulisi* (AM M18833); and D, cranium of female paratype *M. f. fardoulisi* (AM M 18849).

M25050, AM M25051, AM M25054, AM M24055.

Diagnosis. *Melonycteris w. aurantius* differs from *M. w. woodfordi* in being significantly larger (P less than 0.10) in all variables measured except upper cheektooth row length and upper canine length in males, and in postorbital width in females. It further differs in that females are significantly larger than males (P less than 0.10) in postorbital breadth and upper cheektooth row length.

Distribution. Nggela and Florida Islands, Nggela Group, Solomon Islands.

Discussion. The concept of the taxon *aurantius* developed here is quite different from that of Phillips (1966). I regard it to be a subspecies of *M. woodfordi* that is restricted to the Nggela group. It differs from *M. w. woodfordi* primarily in its larger size and in that females are larger than males in most measurements. This latter condition is most unusual in *Melonycteris*, where the majority of taxa show marked sexual dimorphism with males being larger than and morphologically different in cranial morphology from females. The difference in insertion lines for the temporals as described for the sexes of *M. w. woodfordi* however holds true for this subspecies also, with the difference that the males can develop a sagittal crest on the posterior part of the cranium. This may be a function of larger size.

The holotype of *M. w. aurantius* is described in detail by Phillips (1966). He regarded it as being somewhat atypical of his new species, and many of the features that he mentioned in his diagnosis and discussion in fact represent the condition of the paratypes only. This has led to some confusion, as these paratypes differ in important ways from the holotype. Indeed I consider that the paratypes represent a different taxon (*M. w. woodfordi*), from the holotype. The holotype of *M. w. aurantius* is clearly adult. The basilar suture is fused and the animal was lactating when captured. The length of the forearm is given both on the label and by Phillips (1966) as 53.8 mm. However, this cannot be correct. Even as a dry skin the left forearm (the only one easily measurable) is 58.9 mm long, and the right appears to have been of a similar length. Before shrinkage associated with drying out, the forearm would perhaps have been 1 to 2 mm longer. The error in measuring forearm length probably occurred in the field, or it may be a transcriptional error. The correct forearm length of the dry skin is concordant with the forearm lengths of other specimens of this taxon from the Nggela group reported upon here, but differs markedly from that of Phillips' paratypes. These latter are from Choiseul, and the two specimens measured by me have forearm 49 and 51 mm in length. To judge from Phillip's (1966) metrical summary (mean = 49.3, N = 6, R = 42.9-53.8, the largest being the holotype), the forearms of the remaining specimens must be of a similar length or

Fig.8. Study skin of the holotype of *Melonycteris woodfordi aurantius* (BBM 24440).

shorter. The paratypes are all subadult and, to a large extent, the features mentioned by Phillips as being diagnostic for *M. aurantius* are juvenile features seen in all species of *Melonycteris*.

Foremost among these features is postorbital width, which Phillips (1966) gives as being 8 to 9 mm in *M. aurantius*, as opposed to 7 to 7.5 mm in *M. woodfordi*. Postorbital width is typically larger in juvenile *Melonycteris* than in adults. For example, in the sample of *M. w. woodfordi* from Bougainville held in the Australian Museum, postorbital width ranges from 7.0 to 9.3 mm (N = 25), and those with the largest widths are juvenile. This is because the supraorbital process and calvarium separate as the skull lengthens with age, and a constriction is created between these structures, thus forming a narrower postorbital width. Phillips' misunderstanding of this feature was further compounded as he was comparing (in part) individuals of *M. f. mengermani* from Western Province, for which the sexes had been misrecorded, (and which he took to be typical *woodfordi*, see above and below).

A second diagnostic feature mentioned by Phillips is that the premaxillaries do not contact in *M. aurantius*, being separated by a gap of three to four mm, while in *M. woodfordi* they supposedly do contact. Phillips' estimate of the interpremaxillary gap is impossible, for the purported distance is far too great. Three to four mm is the distance between the canines in most *M. woodfordi*; the premaxillae, where they have not yet contacted, are never separated by more than 1 mm. In all species of *Melonycteris* the maxillaries are held only loosely in place, and either abut (in many adults) or are slightly separated but connected by soft tissue anteriorly (in juveniles). This latter condition is seen in the material assigned to *M. aurantius* by Phillips, and thus is a further juvenile feature.

A third feature mentioned by Phillips is that the posterior portion of the skull is deflected ventrally at a more acute angle than in *M. woodfordi*. This again is typical of all juvenile *Melonycteris*, but is not as evident in adults. It is worth emphasising that none of these features are well expressed in the adult holotype of *M. aurantius*, but are evident in the juvenile paratypes.

Finally, Phillips notes that in *M. aurantius* the dorsum is a more bright orange than in *M. woodfordi*. The holotype (which Phillips says is duller than the paratypes), is indistinguishable in colour from specimens that I have referred to *M. w. aurantius* from Nggela, and indeed from the majority of *M. w. woodfordi* specimens examined by me. The paratypes (from Choiseul) are about as bright as the most rufescent individuals of *M. w. woodfordi* in the collections of the Australian Museum, which are from Choiseul and Ysabel. Phillips may have been misled in his comparisons in that the material that he considered to be typical *M. woodfordi* in fact represents *M. f. mengermani* from Western Province, which is less orange in dorsal colouration than *M. woodfordi*.

Melonycteris fardoulisi n.sp.

Figs 7,9-12, Tables 2-5

Etymology. For Mr Emmanuel Fardoulis, whose generosity in supporting mammal research at the Australian Museum has allowed important studies to be carried out into the biology of the mammals of the Solomon Islands, which otherwise could never have been done.

Diagnosis. *Melonycteris fardoulisi* differs from all other species of *Melonycteris* in that dorsum is brownish rather than orange, in that sexes differ in colour, males being darker than females. Further differing from *M. melanops* in lacking white epaulettes, in having brown rather than black fur bases, in lacking claw on digit 2, and in having larger P^1 and M_3. It further differs from *Melonycteris woodfordi* in that males are significantly larger than females (P less than 0.10) in all samples except *M. f. fardoulisi* where the sample size is very small (see below), in condylobasal length and upper cheektooth row length. The disparity between the sexes (with males being larger) in condylobasal length relative to bizygomatic width, and in canine size and morphology, is also greater (Figs 3, 6). A prominent sagittal crest is present in most adult males (in some *M. f. mengermani* it is less prominent).

Discussion. *Melonycteris fardoulisi* occurs as distinctive populations on the larger islands of the eastern Solomons chain, as well as in Western Province. It almost certainly does not occur on Rennell or Belona, nor on the islands of Temotu Province, as our survey, as well as the work of Hill (1956) failed to reveal it there. The populations of Western Province, Malaita, Guadalcanal and Makira are each very distinctive, and that from the Russells may prove to be distinctive when more specimens are forthcoming. These first four populations are here named as subspecies: they are *M. f. fardoulisi* from Makira, *M. f. maccoyi* from Malaita, *M. f. schouteni* from Guadalcanal, and *M. f. mengermani* from Western Province and, tentatively, the Russells.

Melonycteris fardoulisi fardoulisi n.subsp.

Figs 7,10, Table 3

Type material. HOLOTYPE, AM M18833*, adult male skin and skull, caught in a mistnet in secondary forest near Sesena Village (8°31'S 162°05'E), altitude 100-200 m, Makira, Solomon Islands, T. Flannery, 16 Nov. 1987.

PARATYPES, AM M18834, subadult male skin and skull collected, 17 Nov. 1987; AM M18849*, young adult female skin and skull collected, 17 Nov. 1987; AM M18848, juvenile female body in spirits, skull cleaned; AM M20112, entire juvenile female in spirits. Other data as for the holotype.

Additional specimens examined. Makira: AM M23304*,

Fig.9. A, cranium of the holotype male *Melonycteris fardoulisi maccoyi* (AM M18836); B, cranium of paratype female *M. f. maccoyi* (AM M18831); C, cranium of the holotype male of *Melonycteris fardoulisi schouteni* (AM M18841); D, cranium of the paratype female *M. f. schouteni* (AM M18830).

AM M23305, AM M23306, AM M23637*, AM M23638*.

Diagnosis. *Melonycteris f. fardoulisi* differs from *M. f. maccoyi* in abundant pink spotting on the ears, flight membranes and feet. Differs from *M. f. schouteni* and *M. f. mengermani* in that males are significantly larger (P less than 0.10, width across M^1 could not be tested for because of small sample size) in forearm length, condylobasal length (equal variances), zygomatic width (equal variances) canine length, and

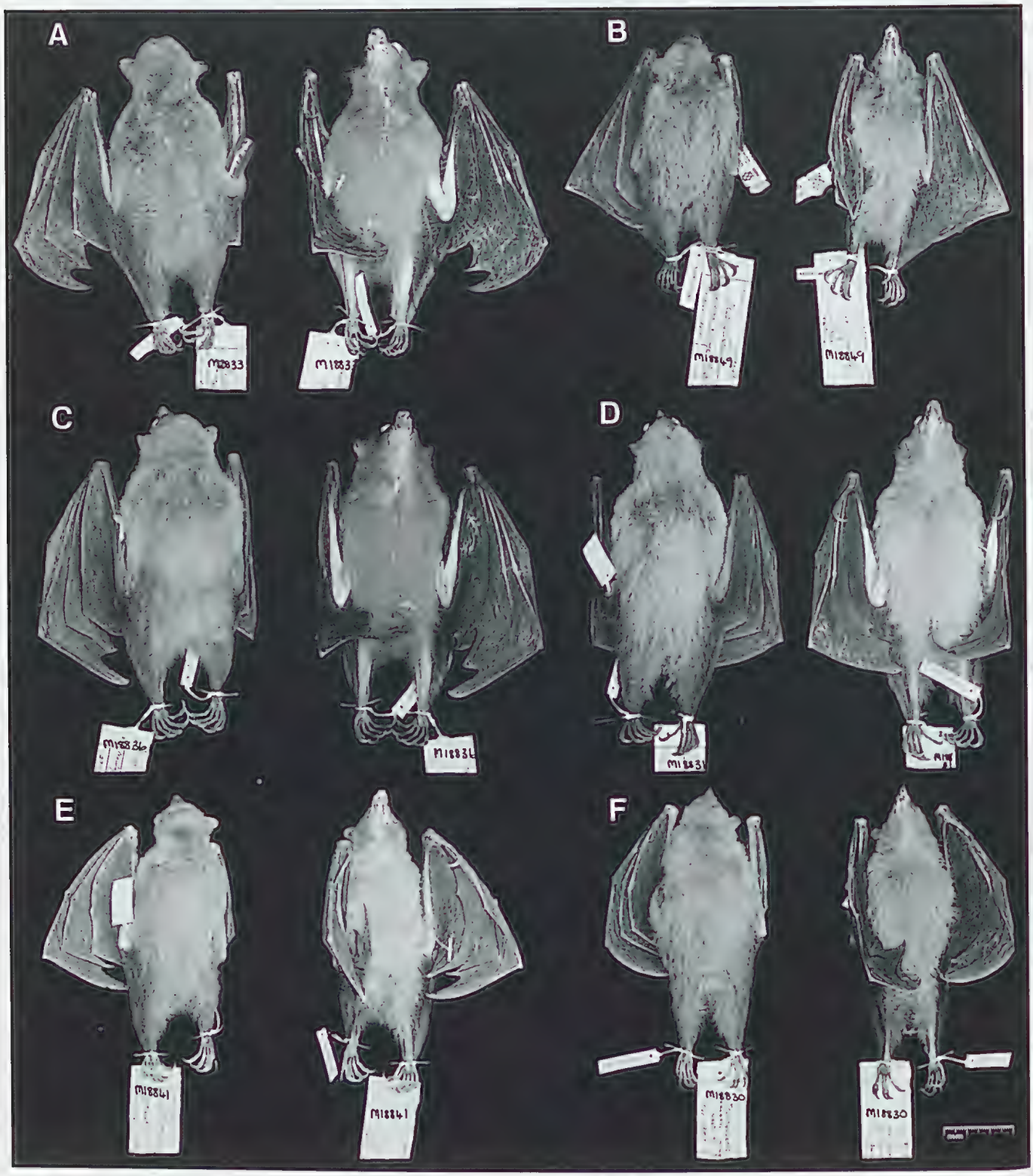

Fig.10. Study skins in dorsal and ventral views of A, holotype male (AM M18833) and B, paratype female (AM M18849) of *Melonycteris fardoulisi fardoulisi*; C, holotype male (AM M18836) and D, paratype female (AM M18831) of *M. f. maccoyi*; E, holotype (AM M18841) and F, paratype female (AM M18830), of *M. f. schouteni*.

from *M. f. mengermani* only in upper cheektooth row length. Females are significantly larger than those of *M. f. schouteni* and *M. f. mengermani* in condylobasal length, and larger than females of *M. f. mengermani* only in forearm length, upper cheektooth row length and (equal variances) width across M^1. Females of *M. f. schouteni* however have a significantly broader interorbital region than in *M. f. fardoulisi*.

Distribution. Makira (San Christobal) Island, Solomon Islands.

Description. *Pelage.* The dorsum and head of the holotype is close to Cinnamon Brown. The venter is Drab. A narrow band of dark hairs is present round the eyes. The ears and feet are black with conspicuous pink spotting. The flight membranes are black, with pink spotting concentrated along the forearm and phalanges. There is no pink spotting on the undersurface of the wings. The claws are dark brown and the muzzle thinly furred. Males are a darker shade of brown than females, being close to Cinnamon Brown or Fuscous, while females are close to Drab or Russet.

Skull. The skull of the holotype is large for a species of *Melonycteris*. There are extremely well-developed sagittal and occipital crests. It differs from the holotype of *M. woodfordi aurantius* (a taxon close in size and geographic location) in the following ways. The rostrum is more elongate and the premaxillaries extend further beyond the canines. The sagittal and occipital crests are extremely well developed. These crests are all but absent in *M. w. aurantius*. The canine is much larger.

The oldest paratype female (AM M18849) of *M. f. fardoulisi*, which still has the basilar suture slightly open, differs from the holotype of *M. w. aurantius* in the following ways. The bizygomatic breadth is much narrower and the occipital crests are even less well developed. The supraorbital processes are extremely poorly developed, and the zygomatic arches are thin by comparison. The braincase is more globose, and the canines are smaller and more gracile.

Discussion. This remains the most poorly known of the subspecies of *M. fardoulisi*. The small sample size (two adult males and three adult females, one of the latter being a young adult) has made statistical comparisons difficult, and it is possible that further differences will emerge as a larger sample becomes available.

The holotype male and a juvenile female paratype (AM M18833, 18848) were taken in a mistnet set in a new garden by a small river situated about 1 km to the east of Sesena Village. The garden contained ripening Papaw, and was backed by dense but disturbed forest. Other Megachiroptera taken on the same night at this location were *Dobsonia inermis* and *Nyctimene* sp. The other specimens of this new taxon were taken in mistnets set on cleared ridgetops and along tracks in disturbed forest. Specimens of *Melonycteris* were rare relative to other Megachiroptera obtained by mistnetting on Makira during 1987; only *Nyctimene* sp. (of which four individuals were obtained) was taken less frequently.

Melonycteris fardoulisi maccoyi n.subsp.

Figs 9,10, Table 3

Type material. HOLOTYPE, AM M18836*, skin and skull of an adult male, collected at Naufe'e Village (10°31'S 161°03'E), altitude 400 m, Malaita, Solomon Islands, T. Flannery, 27 Nov. 1987.

PARATYPE, AM M18831*, skin and skull of adult female, collected at Sinalaggu Harbour, 4 km north of Naufe'e Village, sea level, Malaita, Solomon Islands, T. Flannery, 27 Nov. 1987.

Other specimens examined. Malaita; AM M23457, AM M23577, AM M23814, AM M23817, AM M23818*, AM M23819*, AM M23820*, AM M23821*, AM M23822*, AM M24576, AM M24578, AMNH 99950*. BM24051*.

Etymology. For Mr Mike McCoy of Honiara, without whose help I would have been unable to visit Naufe'e Village, the type locality.

Diagnosis. *Melonycteris f. maccoyi* differs from *M. f. fardoulisi*, and indeed all other *Melonycteris* except some individuals from the Russells, in lacking pink spotting on the ears, feet and wing membranes. It differs from *M. f. schouteni* and *M. f. mengermani* in that both sexes are significantly larger (P less than 0.10) in forearm length and condylobasal length. In addition, males of *M. f. schouteni* are significantly smaller in upper cheektooth row length, canine length, zygomatic width and width across the canines, while males of *M. f. mengermani* are significantly smaller in upper cheektooth row length and upper canine length, and females are significantly smaller in bizygomatic breadth and cheektooth row length.

Distribution. Malaita Island, Solomon Islands.

Description. *Skin.* The skins of the holotype, paratype and referred specimens are similar in morphology. The holotype (a male) is slightly darker in dorsal and ventral colouration than the paratype (a female). Except for some fine pink speckling on the ears, the skin is entirely black in the holotype male. Other specimens are similar except that the paratype has three to four small pink flecks on the forearm, and the additional specimens have between none and eight such tiny flecks on the forearm. The dorsum of the male is close to Drab, but has a less marked brownish suffusion than in *M. f. fardoulisi*. The venter is similar in colouration to that of *M. f. fardoulisi*. Males tend to be darker than females, varying in colour between Drab and Fuscous, while females are close to Russet, but may have Drab underfur.

Skull. The skull of the holotype (male) is similar in morphology to that of the holotype of *M. f. fardoulisi*.

That of the female paratype and referred specimens have the basilar suture fully fused, indicating that they are fully adult.

Discussion. Statistical and non-metric analysis indicates that sexual dimorphism is greater in *M. f. maccoyi* than in *M. f. schouteni*. This dimorphism is a result of the larger size and exaggerated characteristics of males, particularly enlargement of the canine and temporal muscle mass and its associated changes in cranial morphology. The most obvious of these cranial changes are the development of a prominent sagittal crest acting as a firm anchor point for the temporals, and a broadening of the zygoma, allowing for attachment of these large muscle masses to the dentary.

The holotype was taken in a mistnet set near a fruiting forest tree by Sias, a Kwaio assistant. Other Megachiroptera taken in the same mistnet on the same night include *Rousettus amplexicaudatus*, *Dobsonia inermis*, *Macroglossus minimus*, *Nyctimene malaitaensis* and *N. major*. The paratype was taken in a mistnet set near ripening Papaw at sea level. Other species taken in the net included *D. inermis* and *R. amplexicaudatus*. My experience suggests that *Melonycteris fardoulisi maccoyi* is rare relative to other Megachiroptera on Malaita; only *N. major* (of which I obtained but a single specimen) was taken less frequently. *Nyctimene major* usually inhabits small oceanic islands, and its rarity on the mainland of Malaita may be due to competition with *N. malaitaensis*. The rarity of *M. f. maccoyi* on Malaita may be due to forest disturbance, as the species is more common on islands with extensive tracts of primary forest. Malaita is the most heavily populated island in the Solomons chain. Little undisturbed forest remains, and what there is restricted to small patches. Indeed *M. f. maccoyi* was found to be more common in eastern Malaita by Mr P. German in 1990, in an area which is closer to some less disturbed forest.

Melonycteris fardoulisi schouteni n.subsp.

Figs 9,10, Table 4

Type material. HOLOTYPE, AM M18841*, skin and skull of an adult male from Kokaleku Village (9°28'S 159°53'E), altitude 400-500 m, northern Guadalcanal, Solomon Islands. Collected by T. Flannery, 1 Dec. 1987.

PARATYPES, AM M18830*, skin and skull of an adult female; AM M20133, entire female in spirits. Locality and collecting details as for the holotype.

Other specimens examined. Mount Makarakomburu, Guadalcanal; AM M22185*, AM M22186*, AM M22193, AM M22194, AM M22203, AM M22207, AM M22218, AM M22219, AM M22230, AM M22233*, AM M22235, AM M22236, AM M22239, AM M22240, AM M22247*, AM M22251*, AM M22421*, AM M25217, AM M25218: Guadalcanal; BM23831*. BMNH 88.1.5.15*

Etymology. For Mr Peter Schouten, who has, through his art work, so enhanced our understanding of the beauty and diversity of the mammals of Melanesia.

Diagnosis. *Melonycteris fardoulisi schouteni* can be distinguished from *M. f. maccoyi* and *M. f. fardoulisi* in that males are significantly smaller (P less than 0.10, width across M^1 could not be compared with *M. f. fardoulisi* because of sample size) in forearm length, (equal variances) condylobasal length, (equal variances) zygomatic width, and canine length, and from *M. f. maccoyi* alone in upper cheektooth row length. Females are significantly smaller than these subspecies in forearm length and condylobasal length, but are larger than *M. f. fardoulisi* alone in postorbital width. It differs from *M. f. mengermani* in that males are significantly larger in forearm length, condylobasal length and cheektooth row length, while females are significantly larger in condylobasal length, upper cheektooth row length and width across $M^{1\text{-}1}$.

Distribution. Guadalcanal Island, Solomon Islands.

Description. *Skin.* The colour of the dorsum of the holotype male is close to Cinnamon Brown, and very similar to that of *M. f. fardoulisi*. However, the puppet skin of the paratype (female) is markedly lighter, close to Amber. The venter of the paratype female skin is also brighter than that of the holotype male. Males are almost always a darker shade of brown than females, the darkest being close to Fuscous, paler ones being close to Cinnamon Brown. The darkest females approach Cinnamon Brown in colour, and range through to the lightest individuals which are close to Amber in colour. Other aspects of the pelage and external morphology are as in *M. f. fardoulisi*.

Skull. The skull of the holotype (male) is very similar in most respects to that of *M. f. fardoulisi*. However, it differs in its lesser development of the sagittal and occipital crests, and in its smaller size. The canines are not as hypertrophied as in males of *M. f. fardoulisi* and *M. f. maccoyi*, but are still markedly larger than in females. The cleaned skull of the paratype (female) is only slightly smaller than that of the male, and it lacks any suggestion of a sagittal crest, the insertion points for the temporals being separated by almost 6mm in the middle of the calvarium. The occipital crests are barely noticeable. The canines are relatively small and gracile.

Discussion. The three type specimens were taken in mistnets set in newly made gardens near Kokaleku Village, in an area surrounded by largely undisturbed forest. *Nyctimene albiventer*, *Rousettus amplexicaudatus* and *Dobsonia inermis* were taken in the same nets. Other specimens were taken in undisturbed primary montane forest on Mount Makarakomburu, at altitudes of between 380 and 1,270 m. *Melonycteris f. schouteni* is not uncommon on Guadalcanal, but is nonetheless not as commonly caught as species of *Macroglossus*, *Rousettus* and *Nyctimene*.

Melonycteris fardoulisi mengermani n.subsp.

Figs 11,12, Tables 4,5

Type material. HOLOTYPE, AM M22331*, adult male skin and skull, collected 18 Sept. 1990, Vanga Point (7°54'S 156°58'E), Kolombangara Island, Western Province by H. Parnaby.

PARATYPES, AM M22330*, AM M22332*, AM M22333* all adult female skins and skulls, AM M22690* adult male in spirit, skull extracted, AM M22691 female in spirit, skull extracted. Locality and other data same as for the holotype, but collected between 17 and 18 Sept.

Additional specimens examined. Kolombangara: BM23413, BM23414*, BM23434, BM23343, BM23387, BM24423, BM23425, BM23422: Vella Lavella BM23257: New Georgia AM M22325*, AM M22326*, AM M22328*, AM M22334*, AM M22770, AM M22771, AM M22772, AM M22773, AM M22774, AM M22775.

Etymology. A euphonius combination of the surnames of Dr Gregory Mengden and Mr Pavel German, who participated in the 1987 Australian Museum expedition to the Solomon Islands, and contributed greatly to its success.

Diagnosis. *Melonycteris fardoulisi mengermani* differs from all other subspecies in that males are significantly smaller (P less than 0.10) in forearm length, condylobasal length and (equal variances) cheektooth row length, and from *M. f. fardoulisi* and *M. f. maccoyi* in canine length, and from the former alone in zygomatic width. Females are significantly smaller than other subspecies in condylobasal length and cheektooth row width, from all except *M. f. maccoyi* in width across M^{1-1}, and from all except *M. f. schouteni* in forearm length. The sagittal crest of males is usually less well developed than in other subspecies, while the zygomatic breadth is great relative to the condylobasal length in males.

Distribution. *Melonycteris fardoulisi mengermani* has been found on Vella Lavella, Kolombangara, and New Georgia Islands in Western Province (Fig.1). It may also occur in the Russell Group (see below).

Description. *Pelage.* The fur of the venter of the holotype is close to Raw Umber. The skin itself is brown, and the fur of the dorsum of the holotype is close to Cinnamon Brown. In general, individuals are not as dark as they can be in other subspecies of *M. fardoulisi*. Males are usually close to Cinnamon Brown, and females are light in colour, close to Amber or Clay. Although pale, none approach the orange colour of *M. woodfordi*. At

Fig.11. A, cranium of holotype male *Melonycteris fardoulisi mengermani* (AM M22331); B, cranium of paratype female *M. f. mengermani* (AM M22330).

the extremes the colour variants of the sexes approach each other, but in the present samples do not overlap.

Skull. The complete fusion of the basilar suture of the skull shows that the holotype is adult. Apart from its smaller size and more gracile construction, it is similar in morphology to the holotype skull of *M. w. aurantius.* It differs however in the presence of a very slight sagittal crest.

Discussion. Unfortunately there has been some confusion regarding the identity of some of the skulls referred to this new taxon. The confusion centres around two skulls that apparently lost their identification during preparation, and a third which appears to be a female skull associated with a male skin. This latter specimen is BM23434. A note accompanying the remaining two skulls suggests that one is probably the skull of BM23883, the other BM23275 (possibly meant to read BM23257). Whatever the case, these three skulls have been excluded from this analysis, as it is now not possible to be confident about their sex or origin. Indeed, the entire Bishop Museum sample of *M. f. mengermani* should be treated with caution. It appears that considerable confusion between skulls and skins or bodies arose at the time of preparation, and the association of skulls with other remains cannot not be assumed to be correct.

Phillips (1966, 1968) mentions four of the specimens (BM23413-4, 23434, 23275) described here. He regarded them as being *M. woodfordi* from Choiseul. It is unclear how this confusion regarding locality arose, as the specimens are all accompanied by tags bearing the correct locality data. As mentioned elsewhere this misunderstanding contributed to Phillip's misinterpretation of *M. aurantius.*

This subspecies has a wide altitudinal distribution. The Australian Museum expedition to Western Province found it to be common near sea level on Kolombangara and New Georgia, while the Bishop Museum specimens from Kolombangara were collected at an elevation of around 700 m at a location called Gollifer's Camp.

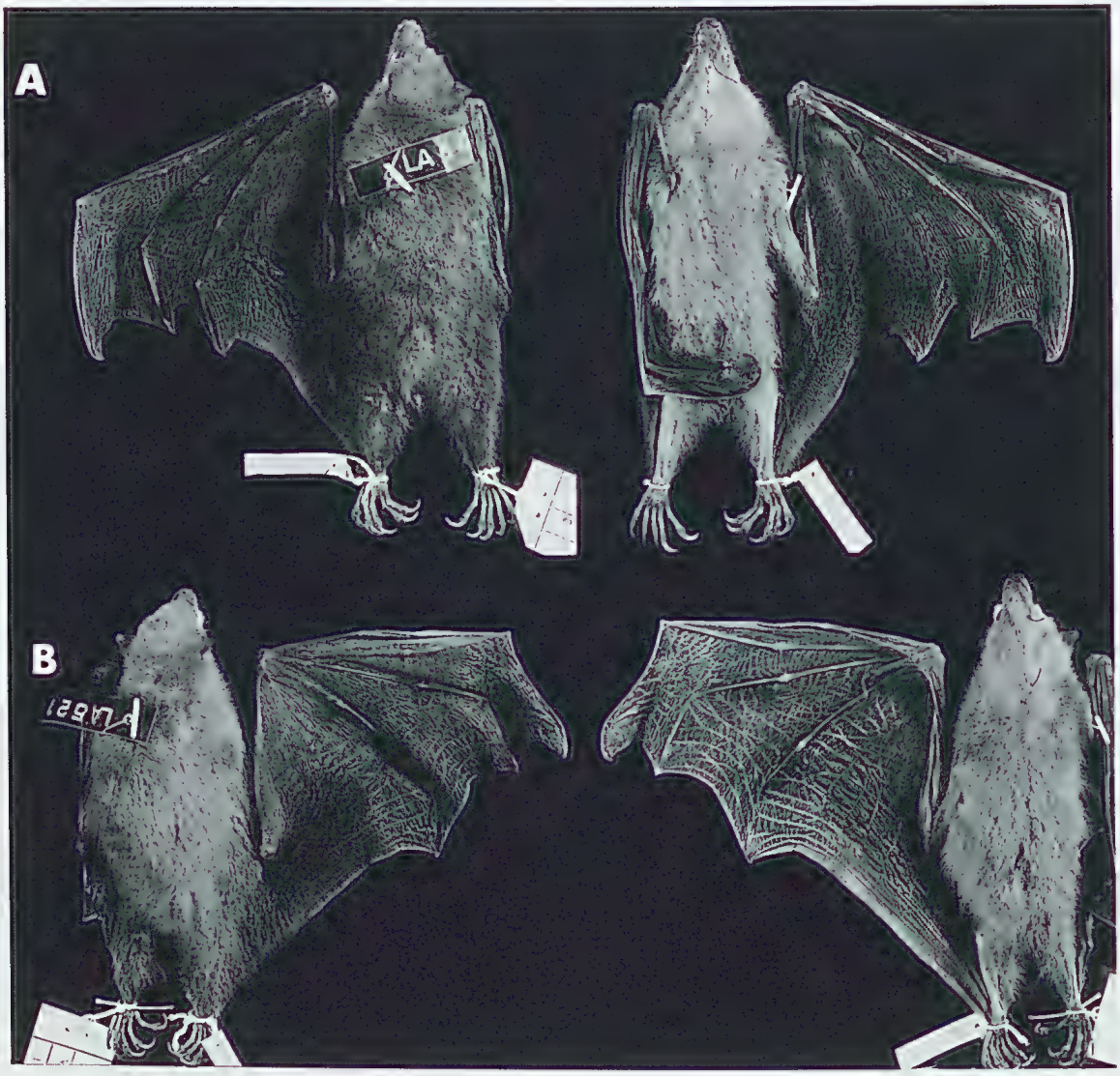

Fig.12. A, study skin in dorsal and ventral view of A, holotype male *Melonycteris fardoulisi mengermani* (AM M22331) and B, paratype female *M. f. mengermani* (AM M22330).

Russell Islands Population. Five specimens (AMNH 79912; BMNH 33.11.11.1, AM M24046, AM M25021, AM M25022) have been collected in the Russell Group. They are tentatively referred to *Melonycteris fardoulisi mengermani*, although their morphology is unusual. There are two distinct colour morphs in the sample. Two of the individuals (AMNH79912, AM M24046) are a uniform dark brown, close to Fuscous, and lacking any pink spotting. Except for their small size, they resemble the darkest individuals of *M. f. maccoyi*. The others are brownish but with pink spots, resembling closely in colour typical *M. f. mengermani*. The sample includes three adult males and one adult female with skulls extracted, all of which could be measured (Table 5). The male sample does not differ significantly (at 0.10) from *M. f. mengermani*. The single female cannot be compared using 't' tests, but it falls outside the range of variability (being larger) of female *M. f. mengermai* (N = 4) in condylobasal length, zygomatic width, upper cheektooth row length and width across M^{1-1}.

Although there are differences in colour in some individuals, and the only known female is clearly larger than any of the measured *M. f. mengermani*, the Russell Islands population is tentatively retained within *M. f. mengermani*. It clearly shows the greatest similarity to that subspecies, although additional material, particularly more females, may well show that it warrants independent subspecific rank. The British Museum specimen was collected on Yandina by Mr Lever in June 1932, and bears a tag stating that it had fallen from a Coconut tree. The American Museum specimen was collected on Pavuvu during the Whitney Expedition by R.H. Beck on 6 August 1927, while the three Australian Museum specimens were collected on Pavuvu by Ian Aujare in April 1991.

Discussion

Phylogenetic relationships. The relationships of the genus *Melonycteris* within the Macroglossinae remain uncertain, which makes it difficult to determine the polarity of many characters within the group. However, because of their distribution and nature, the polarity of some key features is clear. *Melonycteris woodfordi* and *M. fardoulisi* share at least one unquestionably derived feature not seen in *M. melanops*. This is the loss of the claw from digit 2 of the forearm. Contrary to Phillips' (1966) view, this claw is not a mere rudiment that can be easily rubbed off. It is, in my experience a firmly attached claw, invariably present in *M. melanops* but absent in all other taxa. This synapomorphy (claw loss) for *M. woodfordi* and *M. fardoulisi* suggests that they are sister taxa. *Melonycteris melanops* possesses some derived features not seen in other species of *Melonycteris*. These include reduction in the size of M_3 and P^1 (Fig.4) and the presence of a white epaulette on the shoulder (a feature unique within the subfamily). *Melonycteris woodfordi* is unique in the genus in having no sexual dimorphism in most dimensions (*M. w. woodfordi*), or in females being larger (*M. w. aurantius*).

Zoogeography. None of the three species of *Melonycteris* occur in sympatry. The distribution of the various species and subspecies accords well with expectations based upon geography and geological history. The dentally most distinctive member of the genus (*Melonycteris melanops*) is found throughout the Bismarck Archipelago, which is the most isolated part of the range of members of the genus. No subspecies can be recognised at present within this species.

All of the islands known to support *Melonycteris w. woodfordi* are fragments of a much larger landmass that existed when the sea level was lowered during Pleistocene glacial maxima. Diamond (1974) has named this palaeo-landmass Greater Bukida (Fig.1). Thus it seems likely that *M. w. woodfordi* was present throughout most of this landmass during the late Pleistocene, and that since its fragmentation the subspecies has not differentiated greatly morphologically. The only Greater Bukidan fragments that do not support *M. w. woodfordi*, (but which support a closely related taxon) are Nggela and Florida Islands in the Nggela Group, where *M. w. aurantius* is endemic. The Nggela Group have had the most tenuous connection of any of the Greater Bukidan fragments. Seabed topography suggests that the Nggelas would have been the first part of Greater Bukida to have been isolated after the last glacial, around 15,000 ybp. The other islands began to separate between 14,000 and 8,000 ybp. This earlier separation, and the tenuous link between Nggela and the rest of Greater Bukida, may be the reason why *M. w. aurantius* has been able to differentiate there.

Melonycteris fardoulisi is distributed on the long isolated southern and eastern islands of the Solomons chain. There is no evidence that these islands have ever been connected to each other or to any other large landmass. On each of the major islands within its distribution a highly distinctive subspecies has developed.

At the generic level the distribution of *Melonycteris* is unusual in that it is the only mammalian genus to be restricted to both the Solomon Islands and Bismarck Archipelago. Its distribution suggests that the species of *Melonycteris* are not easily able to cross large water barriers as is, for example, the macroglossine species *Macroglossus minimus*, which is distributed throughout the entire region inhabited by species of *Melonycteris* and beyond, but with no evidence of speciation within Melanesia. Some *Melonycteris* are, however, clearly sufficiently vagile for individuals to have crossed the 170 km water gap separating New Ireland and Buka at some time in the past.

Sexual dimorphism. The degree and nature of sexual dimorphism in the species of *Melonycteris* is remarkable. Among bats sexual dimorphism usually takes the form of subtle differences in colouration, body size, or the presence/absence of dermal glands (Hill & Smith, 1984). However, where males are larger than females the males can have greater temporal muscle mass and larger

canines. These latter differences are, however, again usually subtle. Hill & Smith (1984) note that this area of chiropteran biology has received little attention, but that such sexual differences may be related to differing roost and feeding preferences for the sexes.

The pattern of sexual dimorphism described by Hill & Smith (1984) as being most common in bats (slight differences in body size, canine length and temporal muscle mass) is indeed the pattern seen in *M. melanops*. The other species and subspecies however show somewhat different patterns. *Melonycteris woodfordi woodfordi* shows the fewest differences between the sexes, there being no difference in overall size or colour, but males have larger canines and masseter muscle mass (which is reflected in greater zygomatic width and the shape of the parietal ridging on the skull). *Melonycteris woodfordi aurantius* differs from all other *Melonycteris* (and indeed most other pteropodids) in that the usual sexual dimorphism in certain features is reversed, with females being significantly larger than males in condylobasal length, cheektooth row length and postorbital width, but with males still maintaining significantly larger canines and greater zygomatic width. In all populations of *Melonycteris fardoulisi* the sexes differ in colour (the males being darker), males are significantly larger than females in most cranial dimensions and in overall body size; and differences in canine morphology and size, and cranial architecture, are taken to an extreme. Overall, *M. f. schouteni* and *M. f. mengermani*, the subspecies with the smallest body size, show the least degree of sexual dimorphism (although it is still significant), while *M. f. fardoulisi* and *M. f. maccoyi* show the greatest difference between the sexes of any *Melonycteris*. Indeed, so striking is the difference that when I first encountered *M. f. fardoulisi* in the field, differences in colour, size and head shape initially convinced me that males and females represented two different species. This great degree of sexual dimorphism is due to the hypertrophy of male characteristics, the males being larger, having greater sagittal crest development, and larger canines than in the other subspecies. Differences among females of the various subspecies are generally less striking. These general patterns of sexual dimorphism do not seem related to overall size however, and body size bears no relationship to island size in *Melonycteris*.

The varying degrees and nature of sexual dimorphism in the species of *Melonycteris* offer an ideal opportunity to examine the function and significance of sexual dimorphism among bats. For example, a detailed study of the natural history of *Melonycteris woodfordi aurantius* (in which the female is larger) and *M. fardoulisi maccoyi* (where the male is larger), and which occur on similar islands a mere 40 km apart, may go far in answering such questions.

Limited field observations suggest that the sexes of *Melonycteris fardoulisi* may forage separately. For example, during an expedition I undertook to high elevation undisturbed rainforest on the slopes of Mount Makarakomburu in May 1990, 16 *Melonycteris* were obtained. Of these 13 were males and three were females, only one of which was adult. A similarly striking situation was encountered on near Su'u Harbour, Malaita by P. German during the 1991 Australian Museum Solomon Islands Expedition. In secondary forest and garden he collected nine adult *Melonycteris fardoulisi maccoyi*, all of which were female. Further investigations into the capture frequency of the sexes of *M. fardoulisi* may reveal whether these sex ratios are typical of the respective habitats.

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APPENDIX I

Table 1. Forearm length and cranial measurements for island populations of *Melonycteris melanops* (adults only). X = mean, R = range, St = standard deviation, N = sample size, l = length, w = width. * upper cheektooth row length, from anterior of canine to posterior of last molar.

	New Britain		New Ireland		Duke of York
	male	female	male	female	male
Forearm					
X	62	60	64.4	62.2	59.2
R	–	59-61	–	61-63	54.7-63.6
N	2	2	1	3	2
Condylobasal l.					
X	33.6	31.8	33.4	32.3	–
R	–	31.2-32.3	–	31.5-32.7	–
N	1	2	1	3	–
Bizygomatic w.					
X	21.5	18.8	21.1	18.7	19.1
R	–	18.1-19.5	–	18.5-18.9	–
N	1	2	1	3	1
Interorbital w.					
X	7.4	7.2	7.1	6.7	6.2
R	–	6.9-7.4	–	6.5-6.8	–
N	1	2	1	3	1
Postorbital w.					
X	7.6	8.7	7.1	8.3	6.7
R	–	8.6-8.7	–	8.1-8.5	–
N	1	2	1	3	1
Cheekteeth l.*					
X	10.8	11.0	11.6	11.6	11.0
R	–	10.6-11.3	–	11.2-12.1	–
N	1	2	1	3	1
M^{1-1} w.					
X	8.5	8.4	8.4	8.2	8.1
R	–	8.3-8.4	–	8.1-8.4	–
N	1	2	1	3	1
Canine l.					
X	4.7	4.0	4.5	3.8	3.6
R	–	3.9-4.0	–	3.5-4.0	–
N	1	2	1	3	1

Table 2. Forearm and selected cranial measurements for the subspecies of *Melonycteris woodfordi* (adults only). See Table 1 for key.

	M. w. woodfordi		*M. w. aurantius*	
	male	female	male	female
Forearm				
M	54.2	55.2	59.2	59.6
R	50.0-59.2	51.0-60.0	57.7-61.1	58.3-61.8
St	2.11	2.46	1.48	1.27
N	29	14	4	10
Condylobasal l.				
M	30.5	30.7	31.3	32.3
R	29.0-32.1	29.2-32.4	30.3-32.3	30.7-33.1
St	0.84	1.13	0.90	0.80
N	26	14	4	10
Zygomatic w.				
M	19.5	18.5	20.8	19.9
R	17.4-20.6	17.8-19.8	20.0-21.7	19.2-21.0
St	0.86	0.65	0.73	0.56
N	28	15	4	10
Postorbital w.				
M	7.6	7.8	7.0	8.0
R	6.5-8.6	7.0-8.8	6.7-7.4	7.3-9.1
St	0.52	0.52	0.30	0.52
N	30	15	4	10
Cheekteeth l*				
M	10.9	11.0	10.9	11.5
R	10.1-11.6	10.2-12.0	10.6-11.1	10.9-12.3
St	0.38	0.48	0.25	0.49
N	29	14	4	9
M^{1-1} w.				
M	7.9	7.9	8.6	8.6
R	7.1-8.6	7.2-8.4	8.4-8.9	8.2-9.1
St	0.34	0.37	0.24	0.27
N	29	14	4	10
Upper canine l.				
M	4.1	3.5	4.2	3.8
R	3.4-4.5	2.6-4.0	3.6-4.5	3.4-4.2
St	0.34	0.40	0.44	0.26
N	31	15	4	10

Table 3. Forearm and selected cranial measurements for *Melonycteris fardoulisi fardoulisi* and *M. f. maccoyi* (adults only). See Table 1 for key.

	M. f. maccoyi		*M. f. fardoulisi*	
	male	female	male	female
Forearm				
M	61.2	57.8	60.7	57.4
R	57.9-64.6	56.4-59.0	60.6-60.7	56.9-57.8
St	3.35	1.11	0.07	0.45
N	3	5	2	3
Condylobasal l.				
M	32.8	30.8	32.4	31.2
R	32.4-33.1	29.5-32.0	31.8-33.0	30.6-31.8
St	0.35	0.91	0.85	0.60
N	3	5	2	3
Zygomatic w.				
M	20.0	17.9	20.6	17.3
R	19.4-21.0	17.2-18.3	19.8-21.4	17.1-17.6
St	0.90	0.43	1.13	0.25
N	3	5	2	3
Postorbital w.				
M	7.2	7.7	7.6	7.8
R	6.4-8.1	6.9-9.0	6.9-8.3	7.7-7.9
St	0.85	0.81	0.99	0.12
N	3	5	2	3
Cheekteeth l.*				
M	11.4	10.7	11.3	11.0
R	11.1-11.5	10.0-11.5	11.0-11.5	10.5-11.6
St	0.23	0.53	0.35	0.57
N	3	5	2	3
M^{1-1} w.				
M	8.1	7.6	7.8	7.7
R	8.0-8.3	7.3-7.8	7.8	7.5-8.0
St	0.17	0.21	- 0.26	
N	3	5	2	3
Upper canine l.				
M	5.0	3.6	4.9	3.5
R	4.8-5.2	3.3-4.0	4.8-5.0	3.5-3.6
St	0.21	0.30	0.14	0.06
N	3	5	2	3

Table 4. Forearm and selected cranial measurements for *Melonycteris fardoulisi mengermani* and *M. f. schouteni* (adults only). See Table 1 for key.

	M. f. mengermani		*M. f. schouteni*	
	male	female	male	female
Forearm				
M	55.1	53.5	56.9	55.6
R	53.6-57.5	52.4-55.5	55.7-60.0	53.0-58.0
St	1.43	1.42	1.60	2.51
N	6	4	6	3
Condylobasal l.				
M	29.9	28.4	31.1	29.6
R	29.2-31.0	28.2-28.9	29.6-32.1	29.3-30.0
St	0.66	0.32	0.86	0.35
N	6	4	7	3
Zygomatic w.				
M	19.1	17.0	19.0	17.4
R	18.4-19.7	16.6-17.5	18.2-19.9	17.1-17.8
St	0.47	0.39	0.63	0.35
N	5	4	7	3
Postorbital w.				
M	7.2	8.1	7.4	8.0
R	6.8-7.6	7.7-8.7	5.9-8.1	7.9-8.1
St	0.35	0.44	0.77	0.10
N	6	4	7	3
Cheekteeth l.*				
M	10.5	9.9	11.0	10.3
R	10.2-10.7	9.6-10.1	10.5-11.3	10.2-10.4
St	0.24	0.22	0.34	0.12
N	6	4	7	3
M^{1-1} w.				
M	7.7	7.4	7.7	7.8
R	6.9-8.2	7.2-7.5	7.4-8.2	7.7-7.9
St	0.47	0.15	0.29	0.10
N	6	4	7	3
Upper canine l.				
M	4.1	3.3	4.2	3.2
R	3.7-4.4	3.2-3.6	3.9-4.4	2.9-3.7
St	0.27	0.19	0.24	0.46
N	7	7	4	3

Table 5. Forearm and selected cranial measurements for *Melonycteris fardoulisi* cf. *mengermani* (adults only) from the Russell Islands. See Table 1 for key.

	BMNH33.11.11.1	AMNH 79912	AM M24046	AM M25022
Sex	M	M	M	F
FA	54.5	53.3	54.8	54.6
Condylobasal l.	29.4	30.1	29.7	30.5
Zygomatic w.	19.2	19.5	19.2	18.3
Postorbital w.	6.6	6.3	7.5	7.9
Cheekteeth l.*	10.3	9.9	9.5	10.5
M^{1-1} w.	7.8	7.5	7.4	7.7
Upper canine l.	3.9	–	3.5	3.4

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A Revision of the Genus *Lomanella* Pocock and its Implications for Family Level Classification in the Travunioidea (Arachnida: Opiliones: Triaenonychidae)

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ABSTRACT. Genus *Lomanella* Pocock, 1903 is redescribed for type species, *L. raniceps* Pocock, and 18 other species. One new combination is established: *L. inermis (Callihamus)* (Roewer, 1931). Four species groups are recognised on morphological grounds for the six previously described species and 13 new species: *L. raniceps* species group comprises *L. raniceps, L. atrolutea* Roewer, 1915, *L. inermis* (Roewer, 1931), *L. kallista* Forster, 1949, *L. ambulatorio* n.sp., *L. balooki* n.sp., and *L. promontorium* n.sp.; *L. insolentia* species group comprises *L. insolentia* n.sp., *L. revelata* n.sp., *L. troglophilia* n.sp., and *L. alata* n.sp.; *L. exigua* species group comprises *L. exigua* V.V. Hickman, 1958, *L. parva* Forster, 1955, *L. browni* n.sp., *L. thereseae* n.sp., *L. troglodytes* n.sp., *L. quasiparva* n.sp., and *L. blacki* n.sp.; and the *L. peltonychium* species group comprises a single species, *L. peltonychium* n.sp. A lectotype male and paralectotype female are designated for *L. atrolutea*. A key to males is provided. Within the genus, tarsal claws of legs III and IV range from a simple trifurcating claw typical of many triaenonychids, to a complex multiply-branched peltonychium. There is also simplification of penis structure within species of *Lomanella*. The significance of both claw and penis structure to family level classification in the Travunioidea is discussed and it is shown that a subfamily classification of the Triaenonychidae based on claw morphology is difficult to sustain. Three species are known to inhabit caves including a second totally eyeless triaenonychid. The penis of *Nucina silvestris* V.V. Hickman is redescribed as it shows reduction in plates parallelling that in some *Lomanella* spp.

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The genus *Lomanella* Pocock is a group of unusual, highly derived harvestmen occurring predominantly in south-east mainland Australia and Tasmania, but with a single species in the south-west of Western Australia. Favoured microhabitats are under logs and rocks, and in leaf litter or moss. Three species occur in caves, though only one exclusively.

Lomanella belongs to the suborder Laniatores, the most diverse and species rich group of harvestmen in Australia. The Laniatores are characterised by strong raptorial pedipalps (Fig.1) with a movable claw and fixed spines which ensnare and impale prey. Possession of a muscle in the truncus (shaft) of the penis (Fig.11A) places *Lomanella* in the superfamily Travunioidea. In *Lomanella,* this muscle occurs along the length of the truncus (Fig.18G), placing the genus in the family Triaenonychidae. Problems in family level classification are discussed below under "Family Level Systematics".

The nature of the spines on the pedipalp readily distinguishes *Lomanella* from all other Australian triaenonychids: each consists of a short tubercular base terminating with a very long seta (Fig.1, bottom). In other genera, the base is relatively long and spinous and the seta relatively short (Fig.1, top).

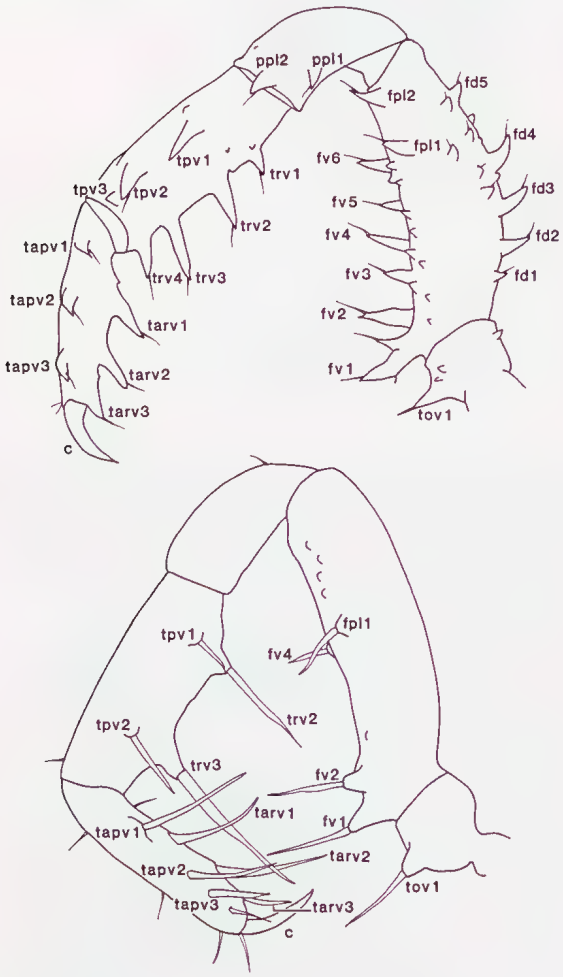

Fig.1. Inferred homology between setae on 'typical' triaenonychid (*Holonuncia cavernicola* Forster) pedipalp (top) and *Lomanella* (*L. thereseae* n.sp.) pedipalp (bottom). tov = trochanter ventral; fd = femur dorsal; fv = femur ventral; fpl = femur prolateral; ppl = patella prolateral; tpv = tibia proventral; trv = tibia retroventral; tapv = tarsus proventral; tarv = tarsus retroventral; c = claw. Not to scale.

Methods and Materials

Type material of all nominal species has been examined and reassessed. The following abbreviations are used to indicate the present location of material: AM – Australian Museum, Sydney (usually denoted by the registration number prefix KS); ANIC – Australian National Insect Collection, CSIRO, Canberra; FIS – Forschungsinstitut Senckenberg, Frankfurt am Main; MOV – Museum of Victoria, Melbourne; QM – Queensland Museum, Brisbane; NHM – Natural History Museum, London; UQIC – University of Queensland Insect Collection, Brisbane; TMAG – Tasmanian Museum & Art Gallery, Hobart; WAM – Western Australian Museum, Perth.

Terminology and methods of measurement in general follow Hunt (1990). Ozopore is used for the opening of the odoriferous gland, lateral plate becomes dorsolateral plate, and shaft becomes truncus in conformity with Martens (1986). However, we use "sensillar region" instead of Martens' term "Sensillentrager" for the area of the glans carrying setae. Tergal areas are abbreviated to TA1, etc.; coxa of leg I is coxa I, claw of tarsus IV to claw IV, etc. Other abbreviations are: SL = scute length, CW = carapace width, PFL = pedipalp femur length, FIV = femur IV length, IOD = interocular distance, TF = tarsal formula. Notation and inferred homologies for pedipalp spination are given in Figure 1. An evaluation of character states has involved an assessment of whether they are plesiomorphic or apomorphic as part of a broader cladistic study of Australian Triaenonychidae (Hunt, in preparation). Measurements of males are usually presented as SL 2.27-2.50 (2.38, 5) which is scute length range (mean, sample size). Means are given for sample sizes of three or more. Normally one female is measured to give an indication of lengths relative to the male. Official numbers for caves (e.g., IB-4) follow Matthews (1985). The cavernicolous species described below are included as undescribed species in Eberhard *et al.* (1991). Table 1 is listed in the Appendix.

Morphology of *Lomanella*

Reference to Figures 1 to 8 provides an overview of characters important in the classification of *Lomanella.* Those considered important in defining the genus and its species groups, and in providing insights into higher classification are discussed here.

Pedipalp spination. Spines on the pedipalp have a short tubercular base terminating in a very long seta (Fig.1, bottom), a condition regarded as synapomorphic for the genus. A long spinose base with a relatively short seta, arising usually subterminally, is plesiomorphic

(Fig.1, top).

Absence of spines from the dorsal surface of the femur and from the patella is synapomorphic for the genus. In *Lomanella*, the most plesiomorphic condition regarding disposition of spines is shown in Figure 1, bottom. Various degrees of spine loss are important at the species level.

Claws III and IV. The most plesiomorphic claw morphology occurs in the *L. raniceps* species group (though see discussion below of Briggs' (1971a) views). This claw consists of a strong median prong flanked at an angle by a pair of smaller lateral branches (Figs 2A, 7A), a condition originally used to define the Triaenonychidae, literally "three-claws".

The *L. insolentia* species group has an additional small, scale-like branch at the base of the each lateral branch (Figs 2B, 7B). The *L. exigua* and *L. peltonychium* species groups have between two and 12 lateral branches which are closely adpressed and form a hierarchy of size: one major branch arises from each side of the median prong and lies in a dorsolateral groove along it; a subsidiary branch arises from near the base of the major branch and lies along it; and so on, until a maximum number of branches is established for a particular species (Figs 2C-E, 7C-G).

Claw variation in *Lomanella* may be regarded as forming a transformation series (Fig.2). Implications for family level classification are discussed below.

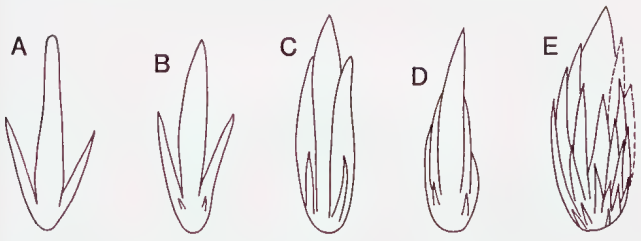

Fig.2. Hypothetical transformation series between a simple trifurcate *Lomanella* claw and a complex peltonychium (although claws of actual species are used, no direct relationship is implied). A = *L. kallista* Forster; B = *L. troglophilia* n.sp.; C = *L. blacki* n.sp.; D = *L. thereseae* n.sp.; E = *L. exigua* V.V. Hickman. Not to scale.

Penis. Extreme attenuation of the truncus (average diameter less than 15% length) is a synapomorphy for *Lomanella.*

Martens (1986) considers that a full complement of plates – dorsal, dorsolateral, and a sensillar region differentiated as a ventral plate – is the primitive triaenonychid condition, a view with which we agree. Loss of the dorsal plate is a synapomorphy for *Lomanella.*

Lomenalla revelata n.sp. has the sensillar region developed as a separate ventral plate (vp, Fig.3A) and represents the most plesiomorphic condition in the genus. Other species show varying degrees of loss of a separate ventral plate and integration of the sensillar region with the stylus. Within the *L. raniceps* and *L. insolentia* species groups, the most apomorphic condition occurs in *L. raniceps* where there is complete integration (Fig.3C).

A synapomorphy for the *L. exigua* species group is a stylus which is sickle shaped in lateral view and which forms an opposing relationship with a midventral structure which is considered here to be a homologue of the median part of the ventral plate (Figs 3D,E, 8D). Within this group, the most plesiomorphic condition occurs in *L. browni* n.sp. (inferior and superior setae separated, sensillar region with wing-like lateral extensions reminiscent of species in the *L. insolentia* species group, midventral distal extension of ventral plate with terminal notch perhaps homologous with the terminal median notch in many triaenonychid genera) (Figs 3D, 21G,H). The most apomorphic species in the group are *L. exigua* Hickman and *L. troglogytes* n.sp. (Figs 3E, 25D,E).

Ovipositor. The *Lomanella* ovipositor has an opening with a row of six to seven elongate, unevenly bifid setae inside each lateral rim (Fig.5H). The triaenonychid ovipositor typically has a fleshy, sometimes sclerotised, lobe on each side into which simple setae are inserted. We are not confident as to whether the lack of conspicuous lobes in *Lomanella* is plesiomorphic or derived. The bifid setae, however, would appear to be derived from simple setae which occur on the ovipositor in all suborders; hence bifid setae are a synapomorphy for the genus.

Position of genital operculum. In most Triaenonychidae, fused sternites 2 and 3 extend anteriorly between coxae IV and thus displace the genital opening anteriad. In *Lomanella*, fused sternites II and III together are subequal in size and shape to sternite IV and lack a mesial anteriad lengthening between coxae IV. The genital operculum in *Lomanella* thus lies relatively posteriad, a condition regarded by us as plesiomorphic.

Size of TA1. In most Triaenonychidae TA1 is much smaller (vestigial) compared with TA2. In *Lomanella* TA1 and 2 are subequal, a condition regarded by us as plesiomorphic.

Lateral lobes on carapace. A prominent convexity on each lateral margin of the carapace above leg II is a synapomorphy for the genus. It opposes dorsal processes on coxa II (which are relatively larger in *Lomanella* than in other genera) and assists in orientating a burst of defensive secretion from the ozopore.

Systematics

Triaenonychidae Soerensen, 1886

The variations in claws III and IV and male genitalia in *Lomanella* analysed above have implications for subfamily classification of the Triaenonychidae. These are discussed in the context of a review of subfamily classifications of the group. Family classification of the Travunioidea is also reviewed.

Subfamily Classification

1. Sternum structure. Roewer (1915) established

three subfamilies on the basis of sternal morphology, namely Triaenonychinae Soerensen, Triaenobuninae Pocock and Adaeinae Pocock. Forster (1954) argued that these taxa were not natural groups (that is, not monophyletic), a view which has gained acceptance. Indeed, there are intermediates between the narrowly based sternum of the Triaenonychinae and the broadly based sternum of the Triaenobuninae, a situation which has led to closely related taxa being placed in separate subfamilies (Hunt, in preparation).

Were this traditional classification in current use, *Lomanella* would be placed in the Triaenonychinae on the basis of the narrow base of its sternum.

2. Structure of claws III and IV. Forster suggested that the Triaenonychidae should comprise two subfamilies based on the morphology of claws III and IV and on biological data: the Triaenonychinae possess claws with a pair of lateral branches shorter than the central prong; the Soerensenellinae Forster possess lateral branches equal to or longer than the central prong and females guard their eggs (Table 1).

Briggs (1969) established a third subfamily, the Paranonychinae Briggs, on the basis of two pairs of short lateral branches. Suzuki (1975b) recognised two further subfamilies. Both possess a multiply-branched peltonychium but, rather than possessing three pairs of

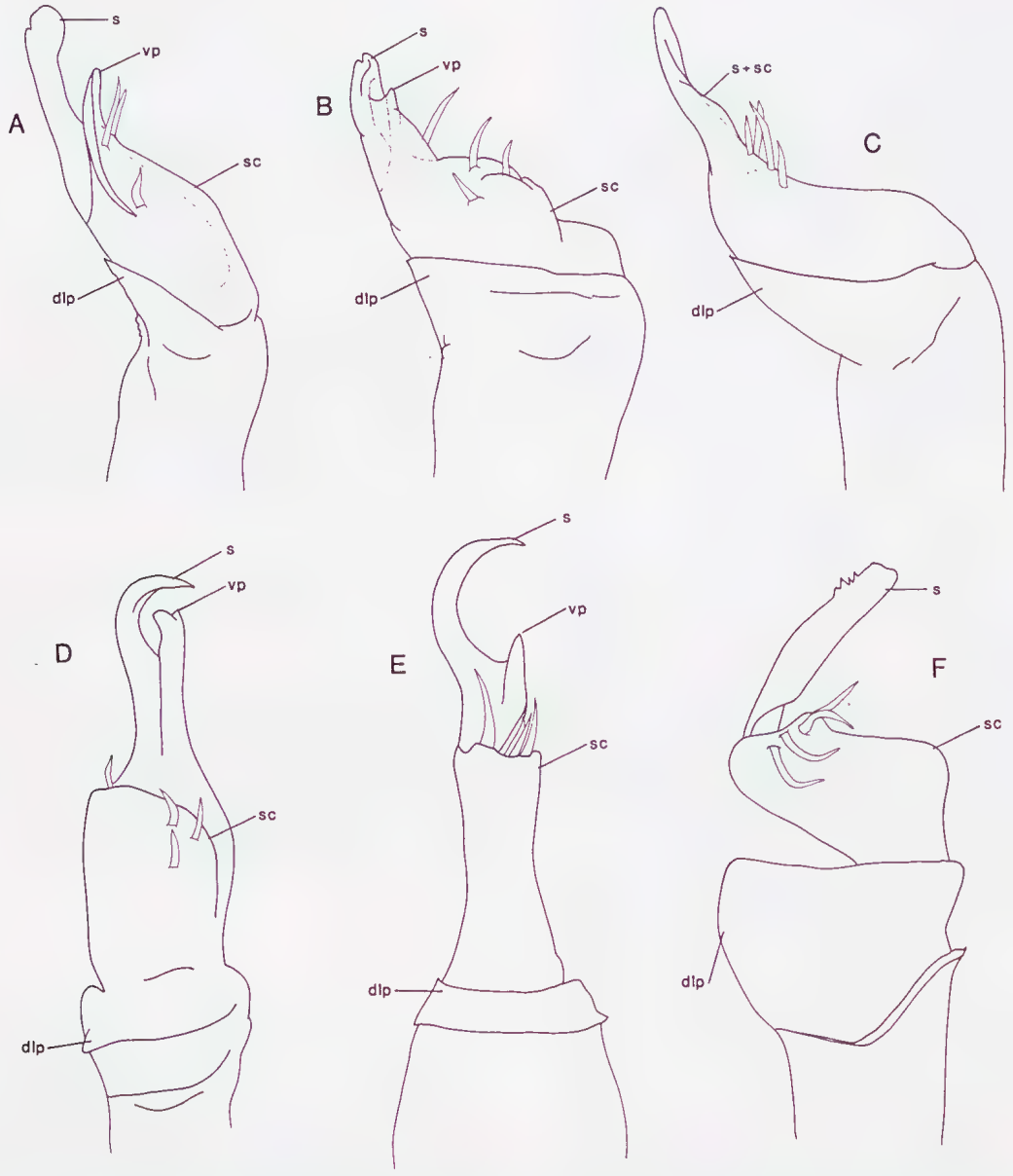

Fig.3. Penis morphology in *Lomanella* spp, lateral aspect. A = *L. revelata* n.sp with well-developed ventral plate; B = *L. balooki* n.sp with vestigial ventral plate; C = *L. raniceps* Pocock with sensillar region completely integrated with stylus and no ventral plate development; D = *L. browni* n.sp. showing presumed, terminally cleft, ventral plate homologue (vp) closely adpressed to stylus; inferior setae and superior seta widely separated; E = *L. exigua* Hickman with reduced ventral plate homologue, sensillar region reduced and all setae forming a close grouping; F = *L. peltonychium* n.sp. with no ventral plate although four setae on each side inserted on a slight mound on sensillar region, stylus clearly differentiated from sensilla carrier. s = stylus; vp = ventral plate; sc = sensillar region; dlp = dorsolateral plate. No dorsal plate present. Not to scale.

lateral branches in juveniles, the Kaolinonychinae Suzuki and the Nippononychinae Suzuki have respectively four and five pairs (Table 1). Briggs (1971a) and Suzuki (1975b) published hypothetical phylogenies of families and subfamilies in the Travunioidea based on claw morphology.

Maury (1988) had difficulty as to subfamily placement of a new cavernicolous Argentinian species, *Picunchenops spelaeus* Maury. It possesses a peltonychium similar to the Triaenonychidae described by Suzuki (1975b). Maury concluded that genital morphology placed the species in this family. He chose not to place the species in a subfamily and expressed reservations about basing a subfamily classification on a potentially labile character (claw structure) that was difficult to study.

Our work on *Lomanella* supports Maury's caution and Shear's (1977) earlier reservations about the heavy emphasis placed on claw morphology. If we were to apply adult claw structure, *Lomanella* would be split into three subfamilies, despite being a well-defined monophyletic group supported by several synapomorphies. Furthermore, *Lomanella* shows a 'transformation series' from simple to complex claw morphology (Fig.2). Juvenile claw structure is also unhelpful – in *Lomanella peltonychium* n.sp., the number of side branches varies according to the instar.

In summary, it is difficult to sustain the use of claw structure in subfamily classification of the Triaenonychidae.

3. Penis morphology. Martens (1986) analyses penis morphology in the Triaenonychidae and discusses, what he considers to be, a strong regional pattern: (i) Australian and South African taxa possess a full complement of plates - dorsolateral, dorsal and a "sensillentrager" differentiated as a ventral plate (1986:fig.2a); (ii) in New Zealand and North American taxa, the dorsal plate is lost and the dorsolateral plate reduced (1986:fig.2b); (iii) in some Japanese taxa, the ventral plate is also lost (Fig.2c); (iv) other North American and Japanese taxa lose even the dorsolateral plate, retaining none of the plates present in Australian and South African taxa (Fig.2d,e). Martens does not include South American triaenonychids in his analysis (see below).

An implication of Martens' work is that penis morphology may be useful in establishing a subfamily classification reflecting zoogeographical patterns. Unfortunately, *Lomanella* morphology argues against this: (i) *Lomanella*, and some other Australian genera, do not possess a dorsal plate and hence do not conform to Martens' view of Australian taxa. Other genera in Australia appear to have retained the dorsal plate but lost the dorsolateral (Hunt, in preparation); (ii) *L. revelata* n.sp. has a "sensillentrager" (sensillar region) developed as a separate ventral plate (vp in Fig.3c). *L. inermis* (Roewer) and *L. balooki* n.sp. retain a vestige of the ventral plate (Fig.3B). *Lomanella raniceps* has lost all trace of a ventral plate (Fig.3C) and closely parallels the structure of *Nippononychus* Suzuki (Fig.2c in Martens, 1986); (iii) *Lomanella* spp. possessing a peltonychium show reduction in the ventral and dorsolateral plates (Fig.3D-F).

Parallel reductions are seen in the distantly related Tasmanian triaenonychid *Nucina silvestris* Hickman (Fig.28) where dorsal and dorsolateral plates are lost and the sensillar region is fused with the stylus without separate development of a ventral plate. *Nucina* shares none of the distinctive synapomorphies of *Lomanella*. This convergence illustrates the potential danger of basing higher level classifications on structures involving loss and/or simplification.

In summary, the biogeography of triaenonychid penis morphology seems more complex than envisaged in Martens' (1986) study. The Australian fauna has several morphologies involving plate retention and loss. A similar situation seems to apply in South America: most species appear to have lost the dorsal plate though Maury and Roig Alsina (1985) indicate its presence, with lack of a dorsolateral plate, in *Ceratomontia mendocina*; some species, for example *Nuncia chilensis* (H. Soares) (= *Chilenuncia donosoi)* and *Nuncia rostrata* Maury seem to possess all plates (Munoz Cuevas, 1971; Maury, 1990).

Family Classification of the Travunioidea

Increasing knowledge about claw structure and other characters has forced reappraisal of family and subfamily classification in the Travunioidea. The Triaenonychidae now include almost every form of claw known for the superfamily (Table 1). Study of *Lomanella* has supported the view that claw characters can be particularly labile (Table 1). Other characters used to support family level taxa, including free lateral sclerites, are now known to be shared across disparate groups.

Of the families discussed by Martens (1986), the Pentanonychidae Briggs is not supported by a unique synapomorphy (Table 1). The peltonychium of the Synthetonychidae is differentiated into branches of different morphologies (for example, the main central pair are broad, flat and tongue-like) but, nevertheless, could be derived from a *Lomanella*-type peltonychium. The bizarre habitus of the Synthetonychidae may support subfamily, rather than family status for the taxon; Martens (1986) believes that penis structure places the group in the Triaenonychidae. Penis structure also argues for sinking the Cladonychidae in the Travuniidae (Martens, 1986).

Family classification of the Travunioidea is resolving into those genera which possess a muscle along the length of the penis truncus (Triaenonychidae) and those with a muscle limited to the base of the truncus (Travuniidae). Even so, the condition in the Triaenonychidae is probably a symplesiomorphy. A search for apomorphic characters, possibly internal, is needed

to help establish a phylogenetic family and subfamily classification.

Although we assign *Lomanella* to the Triaenonychidae, we do not attempt, at this stage, to place it in a subfamily.

Correlation between Claw Structure and Penis Form – a Case of Neoteny?

Although claw structure and penis morphology present difficulties for subfamily classification of the Triaenonychidae, there is nevertheless an interesting correlation between presence of a peltonychium and plate reduction in the penis in various Travunioidea: (i) *Lomanella*, as a group, shows a tendency towards development of a peltonychiun and simplification of the penis; (ii) the penis of *L. raniceps* shows striking similarities to the penis of some Japanese taxa described by Suzuki (1975b), for example *Metanipponony chus* spp. which have a tendency to develop a peltonychium. *L. raniceps*, however, does not carry a peltonychiun though several of its congeners do; (iii) the Synthetonychidae of New Zealand carry a complex peltonychium. Some species, for example *Synthetonychia oliveae* Forster, possess a penis of similar form to *Lomanella revelata* n.sp. in which a ventral plate is present and the dorsolateral plate is somewhat reduced. Other species, such as *S. oparara* Forster, appear to have lost the ventral and dorsolateral plates resulting in an extremely simplified penis, similar in general form to *Mutsunonychus* Suzuki from Japan and *Paranonychus* Briggs from North America, both of which have two or more side branches to the tarsal claw. The penis of *Lomanella exigua* is also greatly simplified (Fig.3E); this species possesses a complex peltonychium; (iv) the Travuniidae possess what is in essence a highly simplified penis; this group has a peltonychium.

The correlation between complex claw and simplified penis does not hold for every taxon. *Picunchenops spelaeus*, for example, combines a relatively complex penis with a peltonychial claw.

There are at least two explanations for an apparent correlation between elaboration of claw structure and simplification of the penis: (i) it points to a close phylogenetic relationship between those taxa where this correlation occurs; and (ii) the taxa are not necessarily closely related; similarities in claws and genitalia are parallelisms which tend to occur together through the mediation of some developmental process.

We favour the latter explanation. The range of variation in *Lomanella*, from simple to complex claws and relatively complex to simplified penis, can be accounted for by evolution occurring independently in Australia. Existing species reveal a transformation series which shows how the most apomorphic extremes could have evolved (Figs 2, 3).

Both claw elaboration and penis simplification may be the result of neotenic processes which tend to affect both structures. Juvenile claws in the Triaenonychidae generally have three pairs of side branches, adult claws one pair. The peltonychium may be an elaboration of the juvenile claw condition. The dorsal, dorsolateral and ventral plates of the penis are laid down towards the end of development; inactivation of the genes responsible may result in an adult penis of juvenilised form.

Rambla (1980) was the first to point out the possibility of neoteny in the Travunioidea. She suggested that the retention of three pairs of lateral branches on the tarsal claw, free lateral sclerites and a free ninth tergite in the adult *Pentanychus* Briggs may be manifestations of neoteny. *Yuria* Suzuki, a triaenonychid from Japan (see note under Table 1), has the combination of a peltonychium, free lateral sclerites, a free ninth tergite and a penis which has lost the dorsolateral and ventral plates. The Travuniidae of North America described by Briggs (1974) combine a peltonychium, free lateral sclerites and a penis of simplified morphology typical of the family. Again, such correlations do not always hold: *Hickmanoxyomma cavaticum* (V.V. Hickman) possesses free lateral sclerites but has a penis carrying dorsal, dorsolateral and ventral plates and has a typical triaenonychid claw (Hunt, 1990).

Both Briggs (1971a) and Suzuki (1975b) consider that the multiply-branched claws and a free ninth tergite are primitive characters and have constructed their phylogenetic trees accordingly. We agree with Rambla (1980) that such characters, if neotenic, are derived rather than primitive. The transformation series in *Lomanella* suggests the peltonychium is a complex, derived structure (Fig.2).

Lomanella Pocock

Lomanella Pocock, 1903: 411.–Roewer, 1915: 83.–Roewer, 1923: 595.–V.V. Hickman, 1958: 11.

Type species. *Lomanella raniceps* Pocock, 1903 by original designation.

Diagnosis. Dorsal surface of pedipalp femur and entire patella without spines; spines on pedipalp composed of a short tubercular base supporting a long seta; prominent distodorsal swelling of cheliceral first segment; carapace with a marked lateral lobe above each ozopore; fused sternites 2 and 3 not extending anteriorly between coxae IV; TA1 subequal to TA2; spiracle not obscured by coxa IV; penis lacking dorsal plate, ventral plate usually reduced or lacking; ovipositor lacking terminal lobes, long, uniform, unevenly bifid setae surrounding vaginal opening.

Redescription. Eyemound often rising 0.3 to 1.0 its length behind anterior margin but sometimes closer; naked or terminating in a short denticle or spine. Anterior margin usually without spines or tubercles above, inter-appendage projections either absent or weakly developed. Carapace laterally above coxa II with enlarged

projection associated with ozopore. Scutal groove distinct mesially; abdomen rounded in form, tergal areas usually marked mesially by depressions and rows of setose granules, TA1 subequal to TA2. Ninth abdominal tergite fused with anal plate; free lateral sclerites absent; scute and free tergites form a smooth (non-crenulated) semicircular rim which over-rides the venter laterally and posteriorly. Sternum long and narrow; genital operculum subtriangular, narrower in males; fused sternites II and III not extending anteriorad between coxae IV; limited movement possible at coxa IV-sternite articulation; spiracle set almost its diameter behind coxa IV. First segment of chelicera lacking a proximal boss, with deep transverse mid-dorsal groove, apical half high and rounded; second segment with a few setose granules, spines lacking. Pedipalp lacking strong teeth, but equipped with long setae each arising from a short tubercular base, proximoventral setose tubercle on femur and retrodistal on tibia largest and always present; dorsum of femur naked; tarsus much narrower than tibia; claw movable. Femur I ventrally usually with row of small setose tubercles/granules, tarsus usually with 3 articles in both sexes, rarely 2. Claws of tarsi III and IV with median prong and one pair of lateral branches forming an angle with it, or with an additional pair of scale-like branches, or with lateral branches adpressed to median prong with one or numerous scale-like side branches, if numerous claw in form of a peltonychium. Juvenile claws III and IV with 3 or more side branches, aroleum absent. Penis long and narrow; dorsal plate absent, dorsolateral plates small and directed dorsad or reduced to an annulus-like rim; ventral plate usually weakly differentiated from stylus or not differentiated as a separate plate, if the latter the stylus + sensillar region broad and plate-like; typically 3 inferior and 1 superior setae, latter reduced and sometimes lost. Ovipositor with circle of long subequal setae around vaginal opening, each seta unevenly bifurcate.

Comments. *Lomanella* as described here is almost certainly a monophyletic group based on several strong synapomorphies. Four lineages are recognised within the genus which we treat as species groups. The differences in leg claw and penis structure between the *raniceps* species group and the *exigua* species group are quite marked and *Lomanella* may eventually resolve into two or more separate, but closely related, genera. Discovery of the male of *L. blacki* n.sp. and examination of its penis should help clarify the situation. Claws III and IV of this species have a structure intermediate between the *insolentia* species group and the *exigua* and *peltonychium* species groups; the *insolentia* species group has a claw structure intermediate between *L. blacki* and the *raniceps* species group (Fig.2).

The affinities of *Lomanella* are obscure; it does not seem closely related to any other Gondwanan genus. Similarities between the simplified penis of *L. raniceps* and Japanese and North American taxa are regarded as parallelisms (discussed above).

The 19 species of *Lomanella* may be separated by the key given below.

Distribution. South-eastern mainland Australia, Tasmania, and the south-west of Western Australia. Eleven of the 19 species occur in Tasmania, six of which can be found in the Gordon-Franklin Rivers drainage basin, south-west Tasmania.

Key to Males of Species in Genus *Lomanella* Pocock

1. Tarsi I and II with 2 articles (Fig.22) 2

—— Tarsi I and II with 3 or more articles 3

2. Penis with 4 long setae on each side ..... *L. parva* Forster

—— Penis with 3 setae, most ventral seta short (Fig.22) ..... *L. quasiparva* n.sp.

3. Blind, no lens or retina visible (Figs 6K, 25A) ..... *L. troglodytes* n.sp.

—— Not blind, lens and retina visible 4

4. Body orange-yellow, little or no pigment, 4 tuberculate setae on pedipalp tibia (Fig.23E), eyemound rounded (Fig.23A) ..... *L. thereseae* n.sp.

—— Body with strong pigmentation pattern (fresh specimens), 3 or less tuberculate setae on pedipalp tibia (if 4, eyemound conical, Fig.27A) 5

5. Tarsus II with 3 or 4 articles 6

—— Tarsus II with 5 articles 8

6. Tarsus II with 4 articles, eyemound with small spine (Fig.26A) ..... *L. blacki* n.sp.

—— Tarsus II with 3 articles, eyemound rounded 7

7. Penis truncus wider than sensillar region (Fig.20C) ..... *L. exigua* V.V. Hickman

—— Penis sensillar region wider than truncus (Fig.21G) ..... *L. browni* n.sp.

8. Eyemound with short spine anterior to eyes or conical (Figs 6H,D,E; 10D; 15A) (female may have spine above or posterior to eyes, Fig.10E) 9

—— Eyemound rounded or with small granule (Figs 6F,G; 9A; 12A,D) 17

9. Anteriolateral corners with small projection or tubercle (Figs 13B, 17B) 10

—— Anterolateral corners smooth 11

10. Body length and SL more than 2 mm ..... *L. inermis* (Roewer)

—— Body length and SL less than 2 mm ..... *L. revelata* n.sp.

11. Pedipalp tibia with 3 or 4 tuberculate setae and femur with fv4 (Fig.27C) 12

—— Tibia with less than 3 tuberculate setae, fv4 lacking (Fig.13A) 14

12. TA1-5 defined by shallow grooves in lateral view (Fig.27A) ..... *L. peltonychium* n.sp.

—— TA1-5 defined by deep grooves (Fig.18A) 13

13. Eyemound rising subvertically just behind anterior margin (Fig.6D) ..... *L. insolentia* n.sp.

—— Eyemound rising steeply some distance behind anterior margin (Fig.18A,C) ..... *L. troglophilia* n.sp.

14. Penis with setae carried distolaterally on sensillar region (Fig.15F,H) ..... *L. promontorium* n.sp.

—— Penis with setae not carried distolaterally on sensillar region 15

15. Sensillar region with broad, parallel-sided wing-like expansions (Fig.14D) ..... *L. kallista* Forster

—— Sensillar region narrows distally (Figs 11B,12H) 16

16. In lateral view, sensillar region with ventrodistal projection (vp in Fig.3, middle top); in ventral view lateral margins of sensillar region not smoothly tapering (Fig.12H) ..... *L. balooki* n.sp.

—— In lateral view, sensillar region without ventrodistal projection (Fig.3, top right); in ventral view lateral margins of sensillar region smoothly tapering (Fig.11B) ..... *L. ambulatorio* n.sp.

17. Scute length (SL) more than 3 mm, dorsum with broad yellow stripe posterior to eyemound ..... *L. atrolutea* Roewer

—— Scute length less than 3 mm, dorsum with or without broad yellowish mesial stripe 18

18. TA1-5 not deeply divided by grooves in lateral view (Fig.4A) 19

—— TA1-5 divided by deep grooves in lateral view (Fig.10D) 20

19. Eyemound rising subvertically immediately behind anterior margin (Fig.19A), dorsum with large mesial yellow stripe/patch ..... *L. alata* n.sp.

—— Eyemound rising more gently a short distance behind anterior margin (Fig.4A), dorsum without large mesial yellow stripe/patch ..... *L. raniceps* Pocock

20. In lateral view, sensillar region with ventrodistal projection (vp in Fig.3, middle top); in ventral view lateral margins of sensillar region not smoothly tapering (Fig.12H) ..... *L. balooki* n.sp.

—— In lateral view, sensillar region without ventrodistal projection (Fig.3, top right); in ventral view lateral margins of sensillar region smoothly tapering (Fig.11B) ..... *L. ambulatorio* n.sp.

Lomanella raniceps species group

South-eastern Australia and Tasmania. Claw of tarsi III and IV with a central prong and 1 pair of lateral branches forming and angle with central prong; tarsus II with 5 articles, free part of stylus (if present) less than 0.3 glans length, stylus and sensillar region almost or completely fused in some species.

Lomanella raniceps Pocock

Figs 4-6, 8

Lomanella raniceps Pocock, 1903: 411.-Roewer, 1915: 84-85.-Roewer, 1923: 595-596.-V.V. Hickman, 1958: 11-13.

Type material. Tasmania: HOLOTYPE male: NHM, G.W. Peckham, no other data.

Other material examined. Numerous specimens from most areas of Tasmania (largely Hickman Collection in AM). Localities include (approximately clockwise from Launceston area): Trevallyn, Flowery Gully, The Sideling near Scottsdale, Mount Barrow, Cascades, Weldborough, Mount Michael, Mount Victoria, Lottah, Saint Columba Falls, Collinsvale, Goulds Country, Myrtle Creek near Mathinna, Mathinna Falls, Douglas River near Bicheno, Nugent, Eaglehawk Neck, Tasman Peninsula, Stonor, Mount Wellington, Highcroft, Arve Valley, Hastings Caves area, Ida Bay caves area, Gordon River area, Franklin River area, Serpentine River, Olga River, Tarraleah, Dee Bridge on Lyell Highway, Lake Saint Clair, Mount Rufus, Rufus Weir, National Park, Navarre River, Pieman River, Hellyer Gorge, Heemskirk Falls, Forth Falls, Wilmot, Liffey, and Burnie.

Diagnosis. Eyemound without spine, covered by small granules, dorsum without large mesial yellow patch posterior to eyes, SL less than 3 mm, sensillar region and stylus completely integrated.

Redescription. MALE. *Body:* SL 2.27-2.50 (2.38, 5 from Trevallyn population); CW 1.37-1.46 (1.42). Dorsal colour dark brown relieved by yellow-orange patches; pigmentation pattern as figured; ventral pattern as figured by Roewer (1923). Eyemound rising about 0.3 IOD behind anterior margin; evenly rounded, unarmed but covered by normal surface granulation (Fig.6F). Scutal groove shallow; TA1-5 not strongly defined by grooves, each with row of small setose granules. Coxosternal region and genital operculum as illustrated (Figs 6B,4C). *Chelicerae* as in Figure 4G. *Pedipalps*: PFL 0.89-1.00 (0.94). Femur dorsally dark brown mottled with yellow and interrupted in distal half by a broad yellow band; patella and tibia yellow distally, dark brown mottled with yellow proximally; tarsus mostly mottled throughout. Size of setal bases are as follows (compare with Fig.1): tov1 tiny, fv1 broad and low, fv2 lacking, fv4 weak, fpl1 very weak, tpv1 and trv2 lacking, trv3 and tpv2 moderately large, tarsus as figured. Seta of trv3 slightly larger than seta of fv1. *Legs*: FIV 1.46-1.60 (1.54). Dark brown, femur, patella and tibia with

subdistal yellow band. Femora only slightly tuberculate ventrally; claw IV three-pronged, a pair of small lateral prongs forming an angle with large central prong; TF 3(2),5(3),4,4. *Penis*: sensillar region not differentiated as a ventral plate but completely integrated with stylus without obvious demarcation. The 3 inferior setae form a close grouping near each ventrolateral margin, superior seta inserted slightly more dorsally.

FEMALE. Similar to male except: pedipalp less robust, genital operculum broader at base, setal bases slightly larger. Ovipositor with six long terminal setae on each side; setae unevenly bifid, the short proximal prongs fringing the vaginal opening (Fig.5H); spermathecae not examined. Key measurements: SL 2.46, CW 1.34, PFL 0.76, FIV 1.45.

Variation. Body size varies across the species range and warrants further study. The terminal part of the penis distal to the setae is long in the holotype and males from northern Tasmania, relatively short in males from southern Tasmania and the mainland population in the Brindabella Ranges, near Canberra (Fig.5). V.V. Hickman's (1958) illustration of a pedipalp shows fv4 lacking.

Comments. Pocock's type is a male, not a female as surmised by Roewer (1915, 1923). Its penis structure suggests it was collected in northern Tasmania. The Trevallyn population near Launceston, northern Tasmania was chosen for measurements; the type measurements SL 2.37, CW 1.47, PFL 0.95, FIV 1.53 fall essentially within the Trevallyn range. The species is widespread in Tasmania though tends to be replaced in the west by *L. atrolutea*. The outlying population on the mainland suggests that the species may have been replaced over

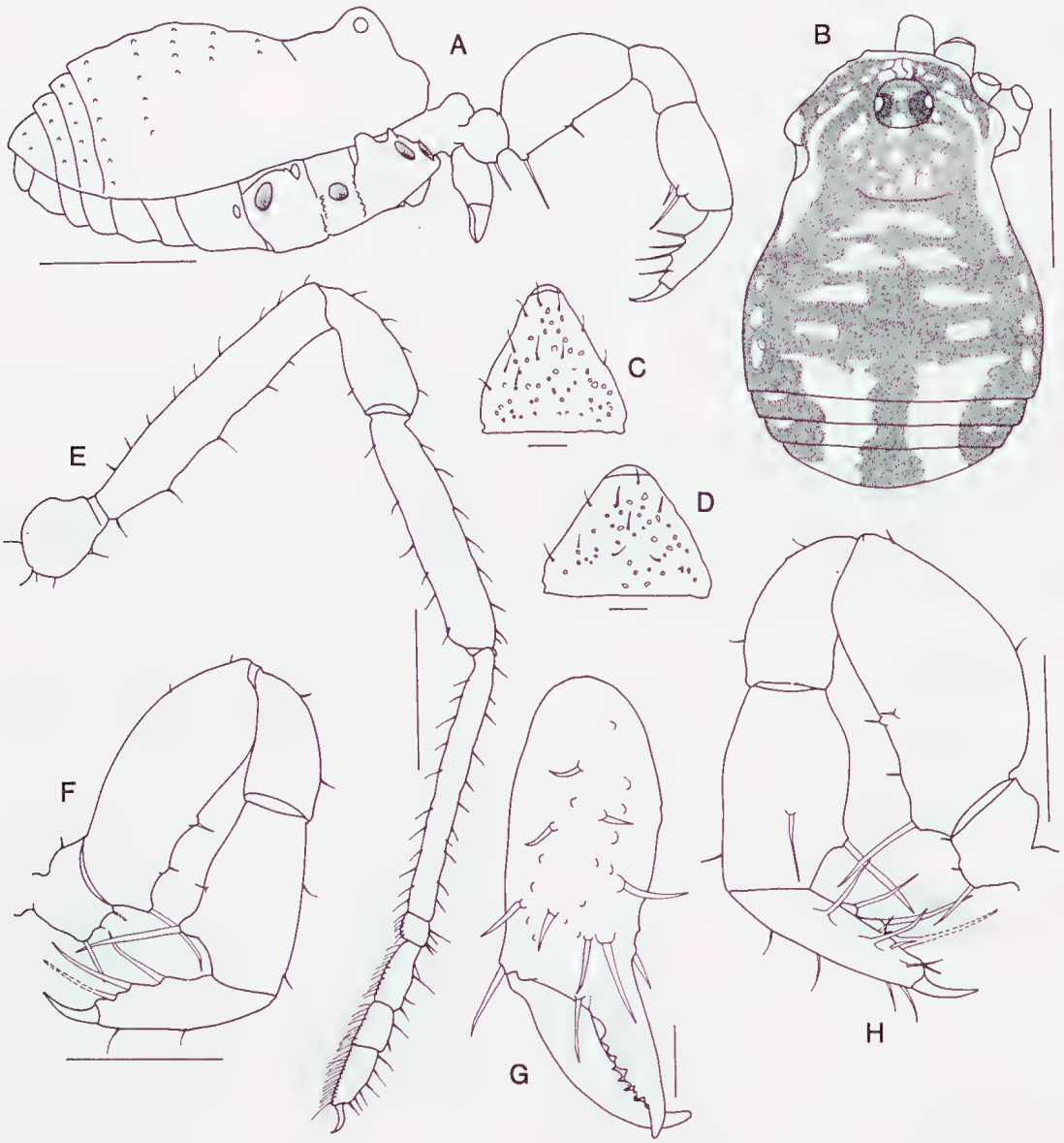

Fig.4. *Lomanella raniceps* Pocock. A,B = holotype male; C,E,G,H = male, Trevallyn population; D,F = female, Trevallyn population. A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C,D = genital operculum; E = right leg I, retrolateral; F,H = pedipalp, retro- and prolateral; G = second segment of right chelicera, dorsal (frontal). Scale bars: A,B = 1 mm; C,D,G = 0.1 mm; E,F,H = 0.5 mm.

much of its mainland range by *L. ambulatorio* n.sp. and related species. Alternatively, the "outlier" could represent a separate sibling species which evolved separately from the morphologically similar Tasmanian species. *Lomanella raniceps* is most closely related to *L. atrolutea* but the latter still shows a trace of join between the stylus and sensillar region. In lacking this join, *L. raniceps* can be regarded as having the most derived penis in the species group (Fig.3).

Natural history. A recent survey of Tasmanian rainforests shows that this species is predominantly ground-dwelling; very few specimens were collected on erect, mossy tree-trunks.

Distribution. Throughout Tasmania; Brindabella Ranges, near Canberra, border of NSW and ACT.

Lomanella atrolutea Roewer

Figs 6,9

Lomanella atrolutea Roewer, 1915: 86-87.–Roewer, 1923: 596.–V.V. Hickman, 1958: 13-15.

Type material. Tasmania: LECTOTYPE male (here designated): FIS, Roewer collection no. 1022, no other data. PARALECTOTYPE female (here designated): FIS, Roewer collection no. 1022, no other data.

Other material examined. Tasmania: KS6917, Daisy Dell, 41°03'S 146°04'E, female, V.V. Hickman, Dec. 1927 (V.V. Hickman's "allotype"); KS6918, Interview River, 41°35'S 144°55'E, D. Kurth, 2 Jan. 1954, male; KS24433, Salmon River Forestry Area, Lerunna Loop site, J.L. Hickman, 27 Nov. 1974, 2 males, 2 females, 1 immature; KS24484, beside Wents Creek below Lake Chisholm, R.B.M. Richardson, 24 Jan. 1974, male, immature; KS24454, side of Duck River at Roger River West, J.L. Hickman, 9 Dec. 1973, 2 males, 2 females; KS23273, Que River Scenic Reserve, 1 km north of Que River Bridge on Murchison Highway, A. & T. Goede, 31 Jan. 1971, 4 males, 8 females, 9 immatures.

Diagnosis. SL more than 3 mm, eyemound without spine and largely devoid of surface granules, dorsum with broad elongate yellow stripe posterior to eyes, fv4 lacking.

Redescription. MALE. Similar to *L. raniceps* except: body larger, SL 3.45-3.80 (3.63, 5); CW 2.13-2.45 (2.30); dorsum with broad elongate yellow stripe posterior to eyes; eyemound set behind anterior margin at distance subequal to IOD, eye circled by small granules, eyemound otherwise smooth (Fig.6G); scutal groove deep, TA1-5 delineated by grooves; pedipalp particularly tibia more elongate and gracile, PFL 1.61-1.97 (1.79), femur almost entirely yellow on proventral surface, tibia with distal

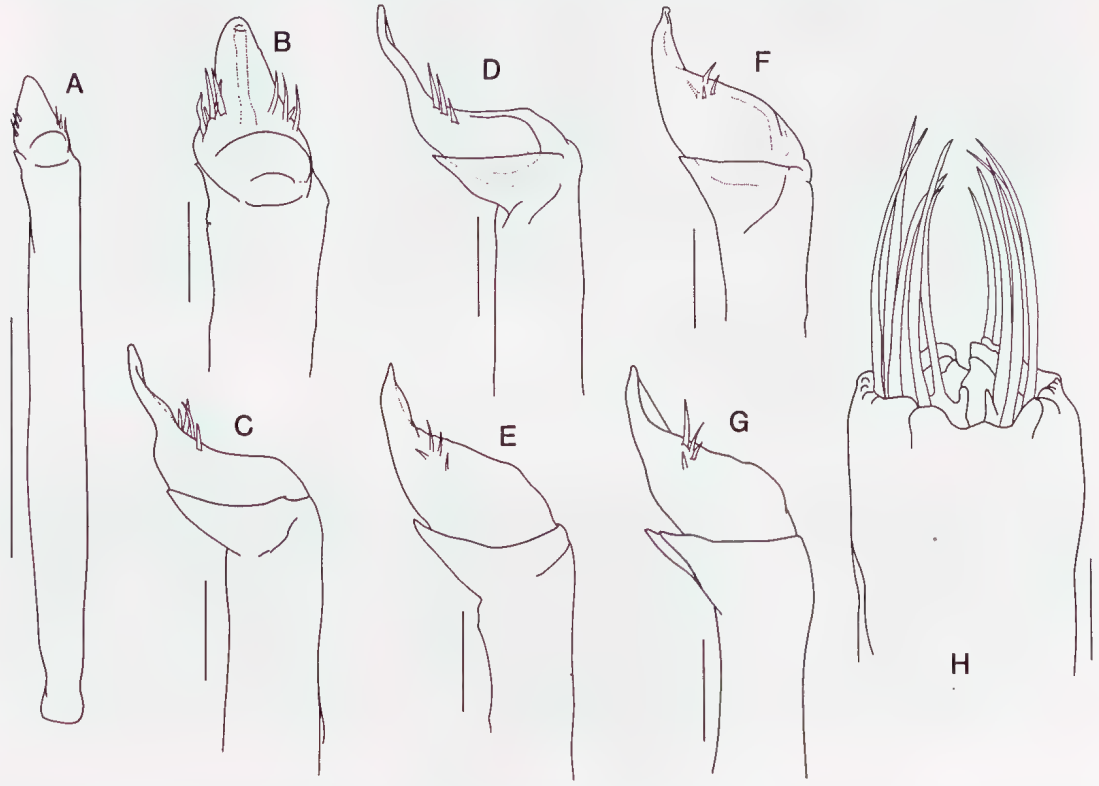

Fig.5. *Lomanella raniceps* Pocock. A-G = male genitalia; H = ovipositor. A-C = holotype male: ventral whole penis, ventral distal & lateral distal respectively; D = *ex* Flowery Gully, northern Tasmania: lateral distal; E = *ex* Arve Valley, south-east Tasmania: lateral distal; F = *ex* near Kutikina Cave, Franklin River valley, south-west Tasmania; G = *ex* Brindabella Ranges, NSW; H = *ex* Trevallyn, northern Tasmania. Scale bars: A = 0.5 mm; B-H = 0.1 mm.

yellow band, fv4 and fpl1 lacking, tarv3 and tapv3 short but relatively stout; FIV 2.58-2.93 (2.70); sensillar region broad in ventral view and tapering to a narrow point which may be the junction with the stylus.

FEMALE. Differs from male as in *L. raniceps*. Key measurements: SL 3.69, CW 2.27, PFL 1.60, FIV 2.63.

Variation. Yellow stripe behind eyemound often with mesial dark brown patches.

Comments. Roewer's (1915) type series comprised a male and female, not two males. Hickman (1958) was not correct in establishing an allotype female. The species is most closely related to *L. raniceps*.

Distribution. Western Tasmania.

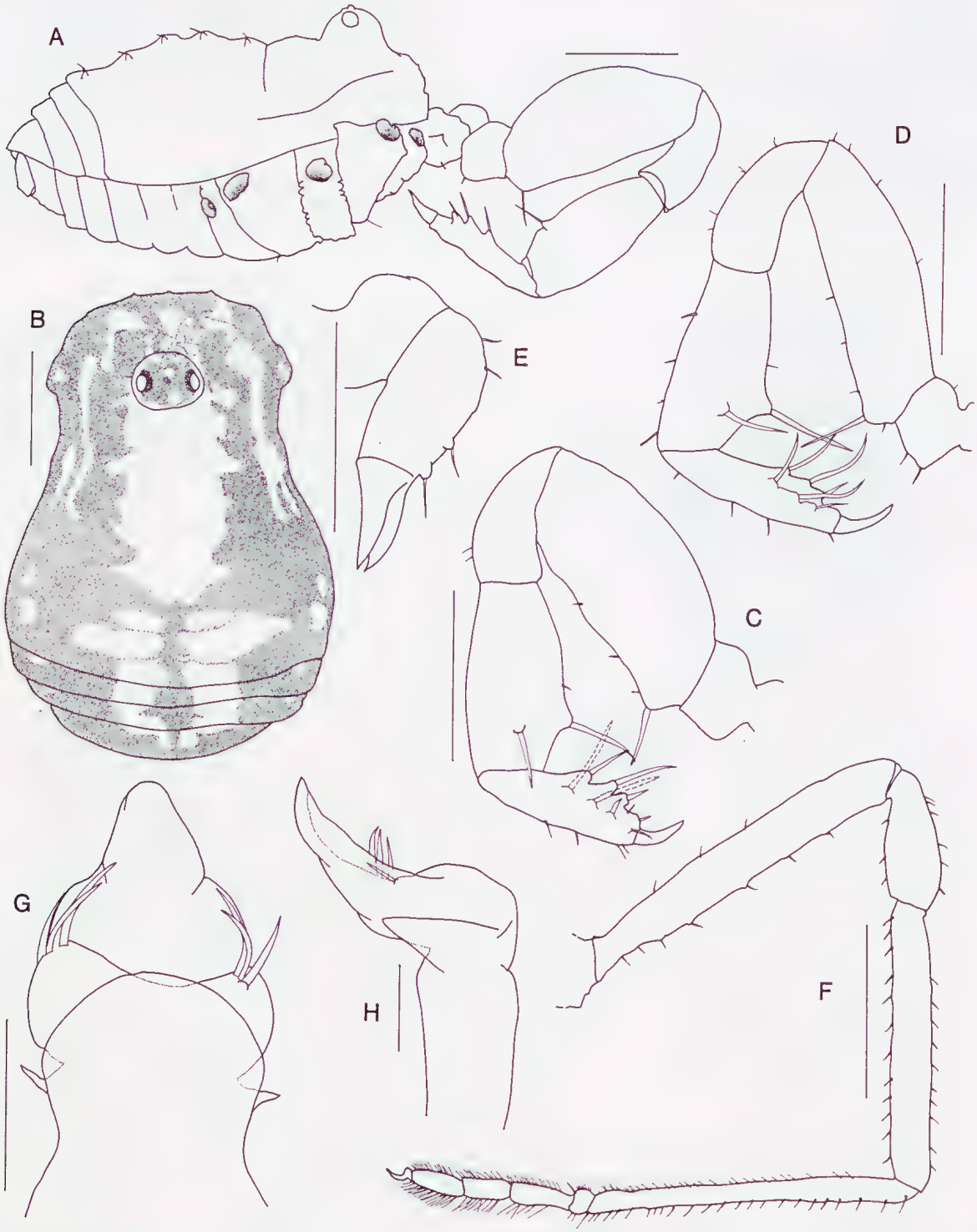

Fig.6. *Lomanella* spp. A-J = female; K = male. A,B = *Lomanella raniceps* Pocock: dorsum & venter, Trevallyn population; C = *L. exigua* V.V. Hickman: dorsum; D = *L. insolentia* n.sp.: body, lateral; E = *L. peltonychium* n.sp.: body, lateral. F-J = eyemound lateral, K = eyemound, dorsal. F = *L. raniceps*; G = *L. atrolutea* Roewer; H = *L. troglophilia* n.sp.; I = *L. exigua*; J = *L. thereseae* n.sp., *ex* Mystery Creek Cave, Ida Bay; K = *L. troglodytes* n.sp. Scale bars: A,B = 1 mm; C-E,G = 500 µm; F,H = 200 µm; I-K = 100 µm.

Lomanella ambulatorio n.sp.

Figs 7,8,10,11

Type material. New South Wales: HOLOTYPE male, KS23229, Geehi, wet sclerophyll forest near bottom of Hannels Spur walking trail, Kosciusko National Park, G.S. Hunt, 29 Dec. 1969. PARATYPES: KS23230, same data, 1 female; KS23231, same data, 2 males, 1 female, 2 immatures; KS23232, Moiras Flat, Hannels Spur, Kosciusko National Park, G.S. Hunt, 29 Dec. 1969, 1 female, 1 immature; KS23233, Tom Groggin, Kosciusko National Park, wet sclerophyll forest, G.S. Hunt, 2 Jan. 1970, 2 males, 1 female; KS23223, Little Peppercorn Hill, Brindabella to Rules Point road, Kosciusko National Park, G.S. Hunt, 28 Dec. 1969, 1 male; KS23225,

Fig.7. *Lomanella* spp. Tarsal claws of leg IV, A-E = dorsal; F-J retrolateral. A = *L. kallista* Forster; B = *L. troglophilia* n.sp.; C = *L. blacki* n.sp.; D = *L. thereseae* n.sp.; E = *L. troglodytes n.sp.*; F = *L. thereseae* n.sp.; G = *L. browni* n.sp.; inset = *L. peltonychium* n.sp.; H = late nymph *L. ambulatorio* n.sp.; I,J = late and early nymphs of *L. peltonychium* n.sp. (the end of the claw in early nymphs is not a simple structure and has the appearance of being plaited). Scale bars: A,E-H = 50 μm; B-D, I,J = 20 μm.

same data, 1 female. Australian Capital Territory: KS23224, Brindabella Range, near Piccadilly Circus, G.S. Hunt, 27 Dec. 1969, 2 males, 2 females; ANIC, 1 km north of Piccadilly Circus, 1200m, C.G. Brooks, 19 Jan. 1970, Berlesate no. ANIC 229, wet sclerophyll, 1 male. Victoria: KS23234, Murrindal-Gelantipy area, wet sclerophyll, G.S. Hunt, 29 Mar. 1970, 2 males; MOV K-1032, same data, male; KS23239, Alpine National Park, 40 km south of Porepunkah, D. Black, 8 Apr. 1990, 1 female; KS23227, Mount Donna Buang, D. Black, 27 May 1990, 1 male.

Other material examined. Victoria: KS23228, Mount Donna Buang; KS23235, 1 km east of Toolangi, Toolangi State Forest; KS23237, 7 km south on Archeron Way, about 15 km east-north-east of Healesville; KS23238, 2 km south on Archeron Way, about 18 km north-east of Healesville; KS23243, 1 km north-east of Toolangi, Toolangi State Forest; KS23246, 4 km north Toolangi, Toolangi State Forest.

Diagnosis. SL about 2.5 mm, eyemound not greatly enlarged in male and occupying about 0.5 length of carapace, in ventral view lateral margin of sensillar region smoothly converging to short spatulate stylus, in lateral view without vestigial lamina of ventral plate.

Description. MALE. Similar to *L. raniceps* except: body slightly larger, SL 2.41-2.70 (2.51, 5); CW 1.49-1.78 (1.60); dorsal pigmentation pattern as figured (Fig.10B); eyemound high and very large, about 0.6 IOD behind anterior margin, armed with a small apical granule; scutal groove moderately deep, extending well towards lateral margin of carapace; TA1-5 strongly defined mesially by grooves; groove between TA4 and TA5 extending almost to lateral margin; PFL 0.98-1.18 (1.07); pedipalp patella yellow, distal half of femur yellow, clearly demarked from dark brown mottled with yellow proximal half; FIV 1.52-1.73 (1.62); leg femora strongly tuberculate ventrally, femur IV much stronger than femur I; stylus in ventral view seen as a spatulate termination to the penis, sensillar region broad but in lateral view not differentiated as a lamina separated from the stylus; inferior setae inserted in concavity and partly concealed in lateral view.

FEMALE. Similar to male except: eyemound much smaller and more removed from anterior margin, different in shape with small tubercle arising posterior to eyes (Fig.10E); pedipalp and femur IV much less robust (Fig.10G), genital operculum broader at base. Key measurements SL 2.70, CW 1.60, PFL 0.98, FIV 1.52.

Variation. The dorsal pigmentation pattern varies throughout the species range. Specimens from the central part of the range (Hannels Spur to Murrindal) have paired yellow-orange patches mesially (Fig.10B), while in the northern part of the range (Little Peppercorn Hill to Brindabella Range), the patches coalesce into a mesial yellow-orange stripe (Fig.10A). Specimens to the south, in the Dandenong Range area east of Melbourne, differ in the following: paired patches occur in TA1 and TA2, but a row of 3-4 patches occurs in TA3 and TA4 (Fig.10C); the pedipalp femur has a yellow band at about 0.5 as in *L. raniceps*, the male eyemound in not as prominent and armed with only a small granule and the spatulate termination to the penis is relatively larger (Fig.11E).

Comments. The differences in colour, eyemound shape and detailed morphology of penis shown by the Dandenong Range specimens may warrant separate species status. They are tentatively placed in *L. ambulatorio* on the basis of similar penis structure. The *L. raniceps* penis form can be easily derived from *L. ambulatorio* by complete incorporation of the spatulate stylus 'vestige' into a stylus-sensillar region complex.

Etymology. The specific epithet is a Latin noun in apposition meaning "walking place". The type locality is near the bottom of the famous Hannels Spur walking trail which descends 1800 m from the summit of Mount Kosciusko to the floor of the Geehi Valley. Most of the known distribution of the species is popular hiking country.

Distribution. New South Wales and Victoria: Brindabella Ranges in the north to Dandenong Ranges in the south.

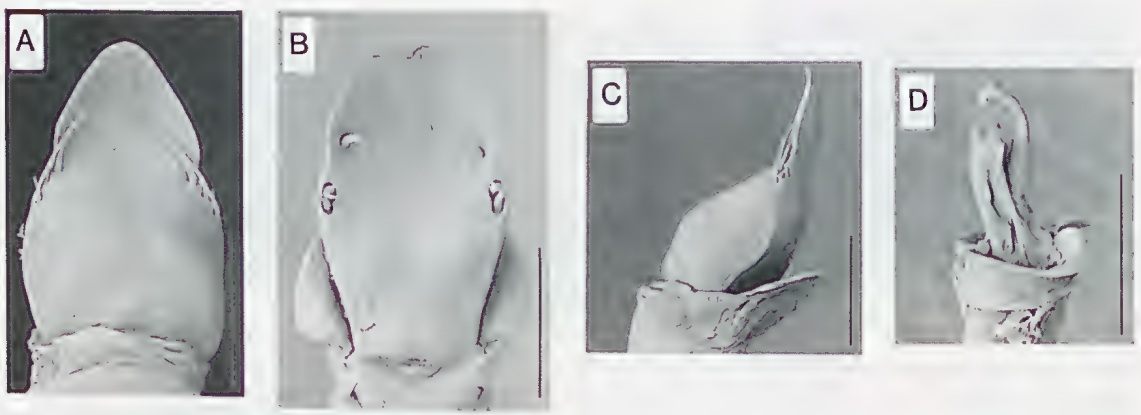

Fig.8. *Lomanella* spp. Terminal part of penis. A,B = ventral; C,D = lateral. A,C = *L. raniceps* Pocock; B = *L. ambulatorio* n.sp.; D = *L. quasiparva* n.sp. Scale bars: A-C = 100 µm; D = 50 µm.

Lomanella balooki n.sp.

Fig.12

Type material. Victoria: HOLOTYPE male: KS23261, 4 km west of Balook, near west entrance to Tarra-Bulga National Park, sieved litter, eucalypt forest, D. Black, 26 Jan. 1990. PARATYPES: KS23262, same data, 1 male, 1 female; UQIC, Mount Baw Baw, eastern Vic., 13 Jan. 1966, T. Weir, 1 male.

Diagnosis. Eyemound with small apical tubercle, penis in lateral view with vestigial lamina of ventral plate, sensillar region in ventral view not parallel sided and not broad distally.

Description. MALE. Similar to *L. raniceps* except: SL 2.31-2.62 (2), CW 1.51-1.79; pigmentation pattern of dorsum as figured; eyemound high and very large, rising very steeply about 0.2 IOD behind anterior margin,

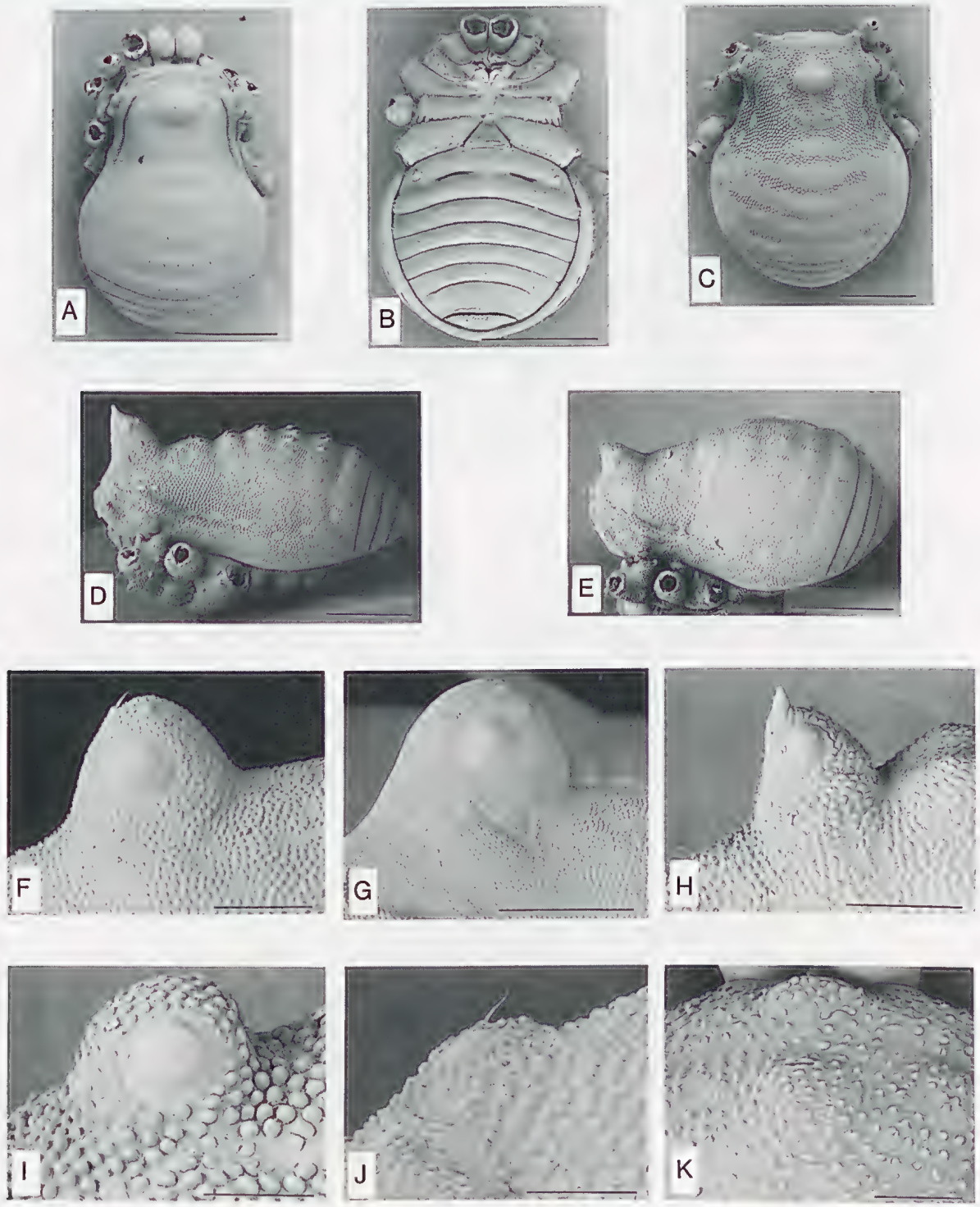

Fig.9. *Lomanella atrolutea* Roewer. B,C,G,H = lectotype male; A,E,F = male KS24454 *ex* Duck River at Roger River; D = female, same data. A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C,D = pedipalp, prolateral; E = chelicera, lateral; F = right leg I, retrolateral; G,H = terminal part of penis, ventral and lateral. Scale bars: A-F = 1 mm; G,H = 0.1 mm.

armed with a small apical tubercle; scutal groove moderately deep; TA1-5 strongly defined mesially by grooves, each TA with row of large setose tubercles; PFL 1.14-1.34; pedipalp patella and tibia without large yellow area in distal half; fv4 lacking; FIV 1.64-1.74; leg femora strongly tuberculate ventrally, femur IV much stronger than femur I; penis in lateral view with a small prominence distal to setae which appears to be a vestigial lamina of ventral plate; 2 pairs of inferior setae inserted on proximal convex part of sensillar region, more distal pair inserted in concave part. In dorsal view, stylus parallel sided and rounded apically; in ventral view sensillar region very broad basally.

FEMALE. Similar to male except: eyemound much smaller and more removed from anterior margin, tubercles on TA1-5 more subdued, pedipalp and femur IV much less robust, genital operculum broader at base. Key

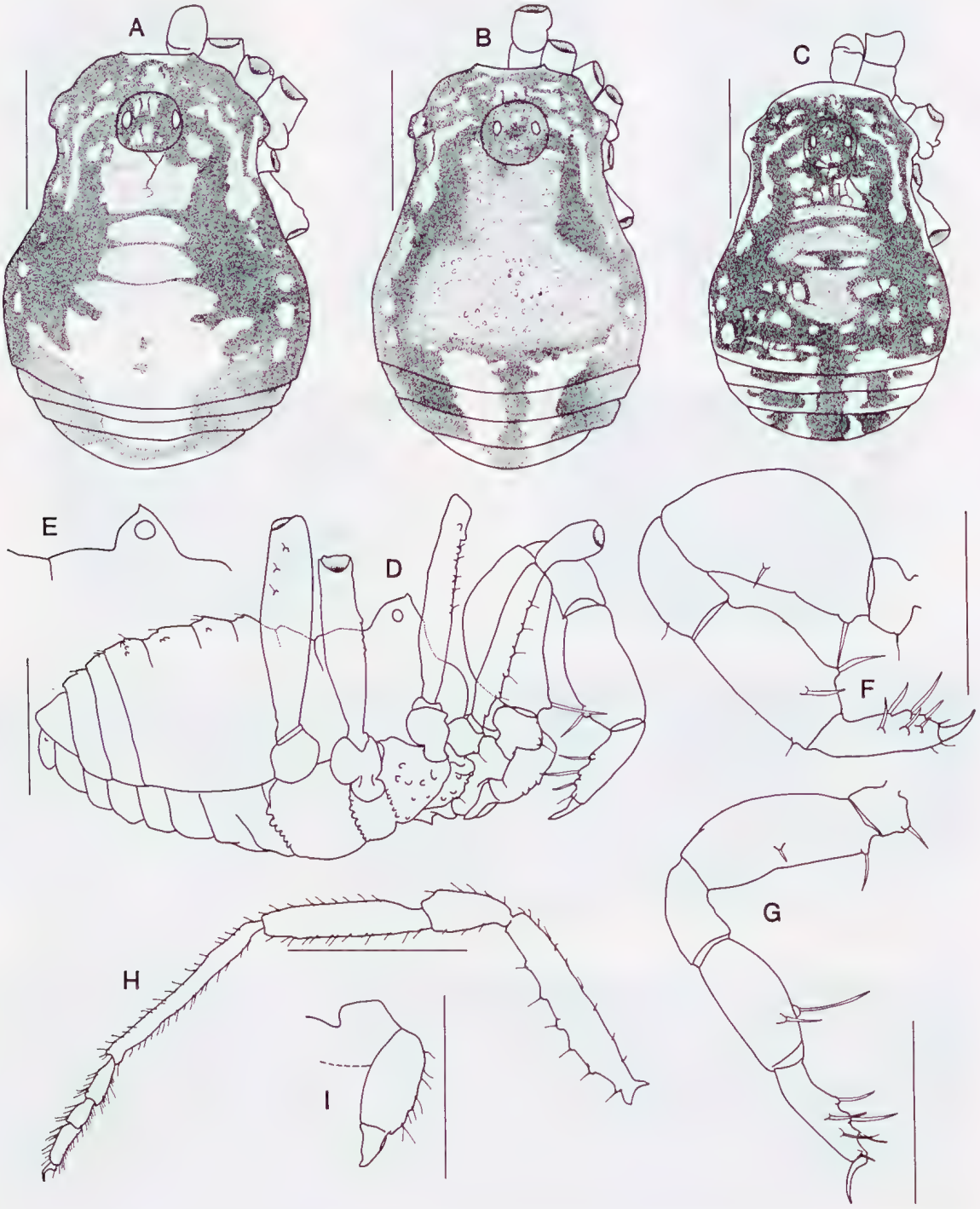

Fig.10. *Lomanella ambulatorio* n.sp. B,D,F,H,I = male KS23231 *ex* type locality; E,G = female KS23230; A = male KS23225 *ex* Little Peppercorn Hill; C = male KS23227 *ex* Mount Donna Buang. A-C = dorsum with pigmentation pattern; D = body and pedipalp, lateral; E = eyemound, lateral; F,G = pedipalp, prolateral; H = right leg I, retrolateral; I = chelicera, lateral. Scale bars: A-H = 1 mm; I = 0.1 mm.

measurements: SL 2.61, CW 1.53, PFL 1.08, FIV 1.59.

Variation. The other male from the type locality has identical genitalia but differs from the holotype in: body smaller, eyemound smaller and set further behind anterior margin, pedipalps less robust.

Comments. The penis of *L. balooki* is somewhat intermediate in form between *L. revelata* which has a well-defined ventral plate and *L. raniceps* which has no expression of a ventral plate. Genital morphology indicates the species is most closely related to *L. inermis* but it lacks processes in the anteriolateral corners of the carapace.

Etymology. The specific epithet is a latinised genitive of the type locality, Balook.

Distribution. Eastern Victoria.

Lomanella inermis (Roewer), n.comb.

Fig.13

Callihamus inermis Roewer, 1931: 162.–V.V. Hickman, 1958: 49-50.

Type material. Tasmania, Hobart: HOLOTYPE male: Roewer coll. no. 1300/42, no other data.

Other material examined. Tasmania: KS6897, Surprise Valley, Lyell Highway, V.V. Hickman, 23 May 1954, 1 female (V.V. Hickman's "allotype").

Diagnosis. SL more than 2 mm, eyemound with short apical spine/tubercle, anteriolateral corners of carapace each with process directed forward, penis in lateral view with vestigial lamina of ventral plate.

Redescription. MALE. Similar to *L. raniceps* except: body larger, SL 2.73, CW 1.80; pigmentation pattern of dorsum as in Figure 13B; eyemound rising about 0.5 IOD behind anterior margin, armed with a small apical spine/tubercle; anteriolateral corners with process directed forward; scutal groove deep and extending almost to lateral margins; TA1-5 strongly defined mesially by grooves, each TA with row of setose tubercles; PFL 1.08; fv4 lacking; FIV 1.67; leg femora strongly tuberculate ventrally, femur IV much stronger than femur I; penis in lateral view with a small prominence distal to setae which appears to be a vestigial lamina of ventral plate, stylus with clear demarcation from sensillar region; 2 pairs of inferior setae inserted on proximal convex part of sensillar region, more distal pair inserted in concave part.

FEMALE. Similar to male except: eyemound much closer to anterior margin, tubercles on TA1-5 reduced to granules, pedipalp less robust, genital operculum broader at base. Key measurements: SL 2.94, CW 1.54, PFL 0.92, FIV 1.58.

Comments. This species possesses all *Lomanella* synapomorphies and clearly does not belong in *Callihamus* Roewer, a nominal genus with close affinities to *Calliuncus* Roewer (Hunt, in preparation). V.V. Hickman (1958) incorrectly refers to the female he

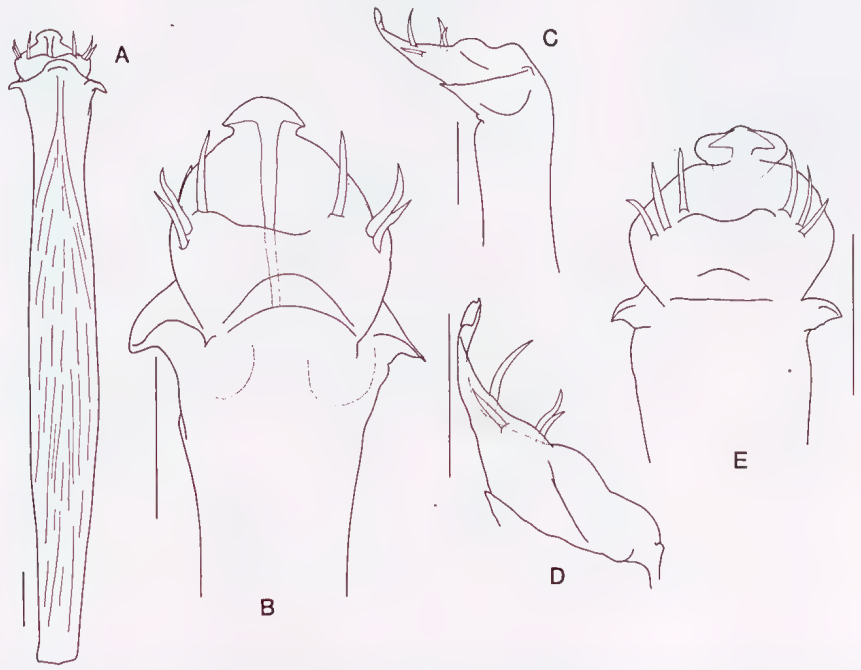

Fig.11. *Lomanella ambulatorio* n.sp. Penis. A-D = KS23231 *ex* type locality; E = KS23227 *ex* Mount Donna Buang. A = entire penis showing muscle in truncus, ventral; B = terminal part, distoventral aspect; C,D = lateral; E = ventral. Scale bars: 0.1 mm.

described as an "allotype". His illustration shows, correctly, a broken eyemound spine. He infers, perhaps correctly, the existence of a much longer spine than is present in the holotype. The difference between the holotype and Hickman's female in the placement of the eyemound (and possible difference in eyemound spine size), may represent specific rather than sexual dimorphic variation.

The penis of *L. inermis* is somewhat intermediate in form between *L. revelata* which has a well defined ventral plate and *L. raniceps* which has no expression of a ventral plate. Genital morphology indicates the species is most closely related to *L. balooki*.

Distribution. Southern Tasmania.

Lomanella kallista Forster

Figs 7,14

Lomanella kallista Forster, 1949: 80-82.

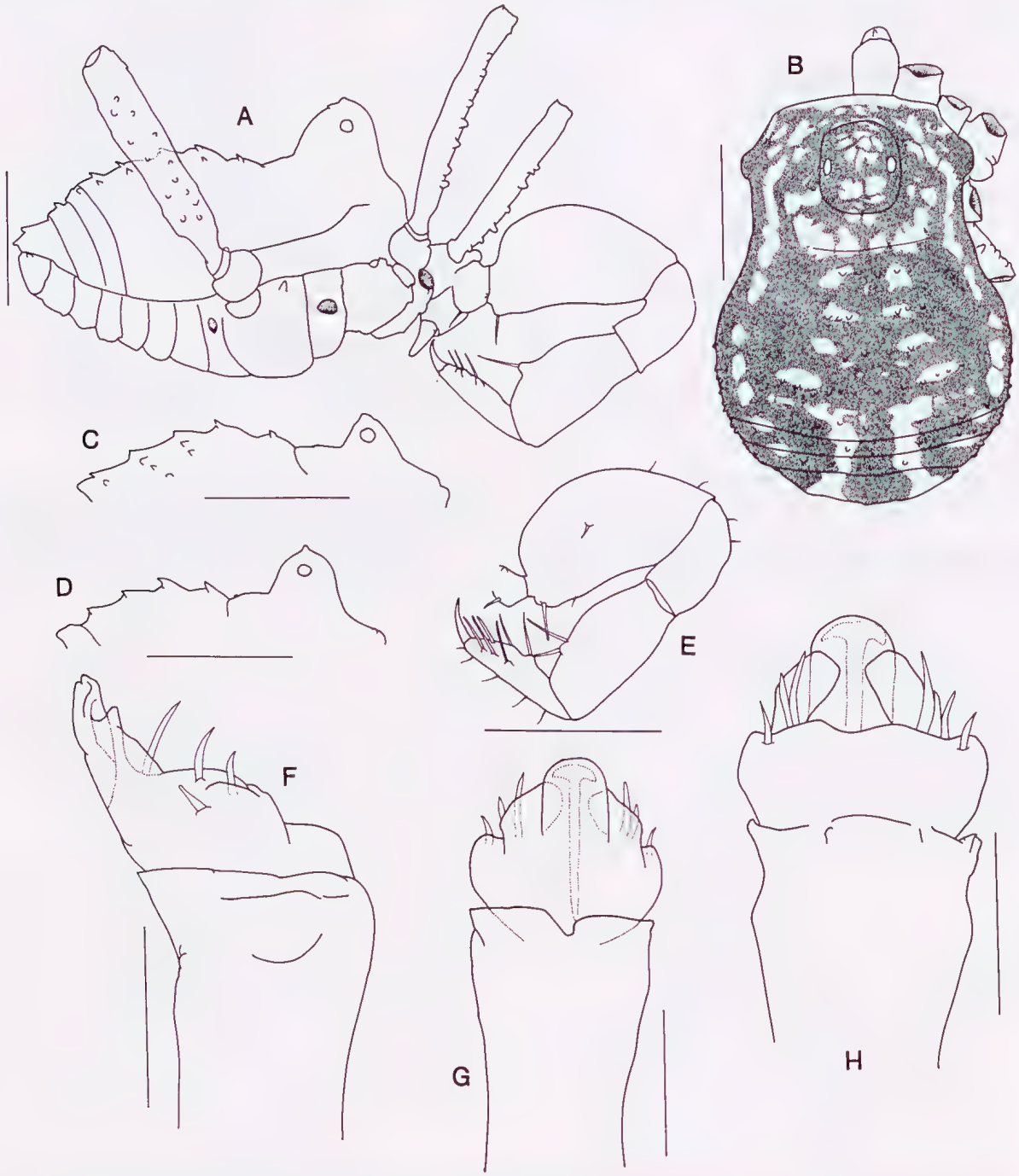

Fig.12. *Lomanella balooki* n.sp. A,B,E-H = holotype male; C = female KS23262; D = male KS23262. A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C,D = scute profile; E = pedipalp, retrolateral; F-H = terminal part of penis, lateral, dorsal and ventral. Scale bars: A-E = 1 mm; F-H = 0.1 mm.

Type material. Victoria: HOLOTYPE male: MOV K-1031, Kallista, 37.53'S 145°22'E, under log, 18 Sept. 1948, A.N. Burns.

Other material examined. Victoria: KS23226, 1 km north of Kallista, sieved tree fern litter, D. Black, 11 Feb. 1990, male, 2 females; KS 23236, 7 km south on Archeron Way, 15 km east-north-east of Healesville, 37°34'S, sieved tree fern litter, D. Black, 4 Mar. 1990.

Diagnosis. Eyemound with small apical spine/tubercle, sensillar region in ventral view parallel sided and broad distally, stylus narrow and directed distodorsally.

Description. MALE. Similar to *L. raniceps* except: body larger, SL 2.62-2.89 (2.73, 3), CW 1.66-1.78 (1.70); dorsal pigmentation pattern as figured by Forster, lateral as in Figure 14A; eyemound high and very large, rising very steeply about 0.75 IOD behind anterior margin, armed with a small apical spine/tubercle; scutal groove moderately deep and extending more towards lateral margins; TA1-5 strongly defined mesially by grooves, each TA with row of large setose tubercles; PFL 1.63-1.87 (1.78), pedipalp tibia without large yellow area in distal half; fv4 lacking; FIV 1.63-1.87 (1.78); leg femora strongly tuberculate ventrally, femur IV much stronger than femur I; sensillar region in ventral view very broad, the alate distal part apparently homologous with lamina of ventral plate; stylus clearly differentiated from sensillar region, narrow and directed distodorsally; superior seta inserted proximally on each dorsolateral flank of sensillar region (Fig.14D).

FEMALE. Similar to male except: eyemound much smaller but apical spine larger (Fig.14B), tubercles on TA1-5 more subdued, pedipalp and leg IV femur much less robust, genital operculum broader at base. Key measurements: SL 2.72, CW 1.57, PFL 1.11, FIV 1.66.

Comments. The penis form of *L. kallista* is somewhat intermediate between *L. revelata* which has a well-defined ventral plate and *L. raniceps* which has no expression of a ventral plate. The species is very closely related to *L. ambulatorio, L. promontorium* and *L. balooki*, differing from each in penis morphology.

Distribution. Victoria: Kallista area near Melbourne.

Lomanella promontorium n.sp.

Fig.15

Type material. Victoria: HOLOTYPE male: QM, Wilsons Promontory, Mount Oberon berlesate, 28 Jan. 1967, G.

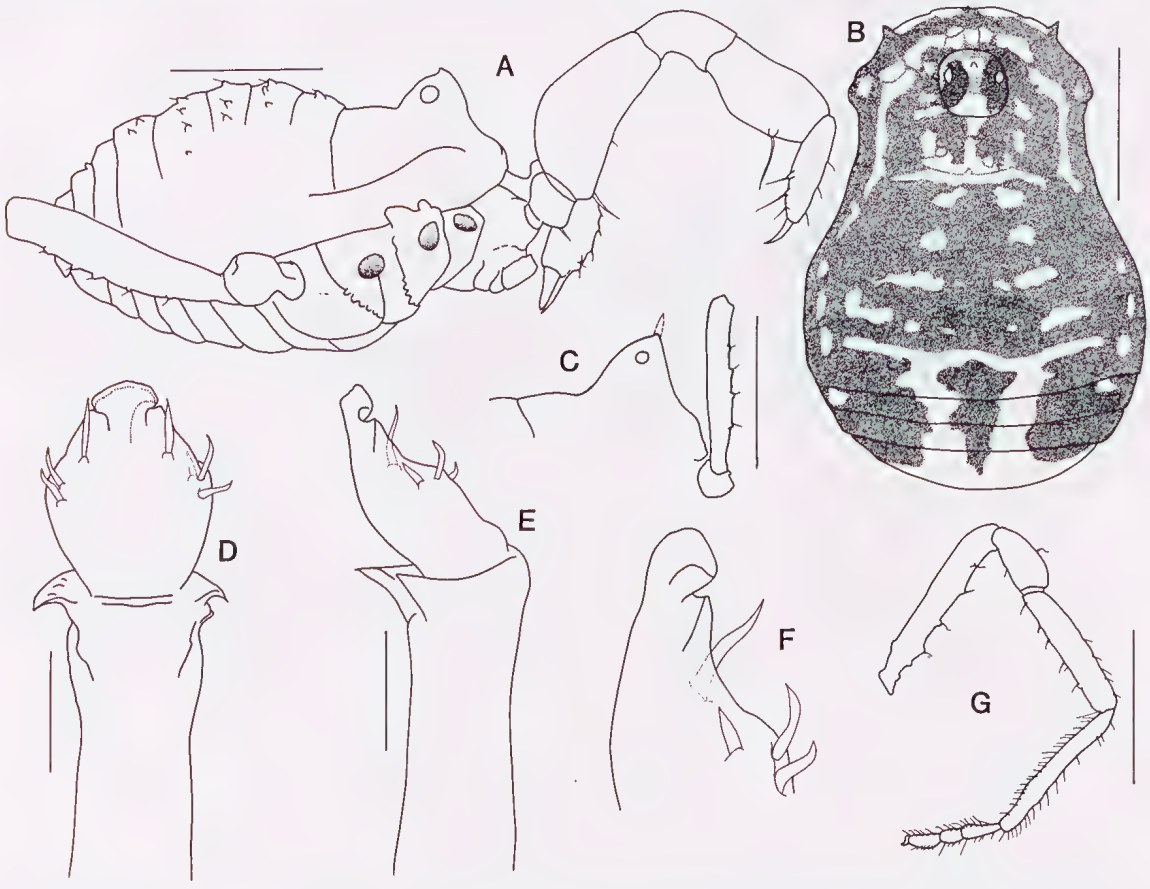

Fig.13. *Lomanella inermis* (Roewer) n. comb. A,B,D-G = holotype male; C = female KS6897. A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C = anterior part of body, profile; D-F = terminal part of penis, ventral, lateral and lateral detail. Scale bars: A-D = 1 mm; E-G = 0.1 mm.

Ettershank.

Diagnosis. Eyemound with small apical tubercle, setae on penis short and placed distolaterally on sensilla carrier, sensillar region with distal lamina lying *ventral* to inferior setae.

Description. MALE. Similar to *L. raniceps* except: body larger, SL 3.02, CW 1.92; pigmentation faded in preservation but appears similar to *L. balooki*; eyemound high and very large, rising very steeply about 0.5 IOD behind anterior margin, armed with a small apical tubercle; scutal groove moderately deep; TA1-5 strongly defined mesially by grooves, each TA with row of large setose tubercles; PFL 1.44, PFL:CW 0.75, pedipalp fv4 lacking; FIV 1.92; leg femora strongly tuberculate ventrally, femur IV much stronger than femur I; penis in lateral view with a sharp lamina immediately ventral to, and arising proximal to, the 3 short inferior setae (may be homologous to the lamina part of the ventral plate but this normally lies distodorsally to setae); in lateral view inferior setae lie serially behind each other, superior seta lies more dorsally; in ventral view sensillar region expands gradually from base and distally extends as a broadly rounded lamina lying ventral to inferior setae.

FEMALE. Not known.

Comments. *Lomanella promontorium* is most closely related to *L. kallista* but penis differs in having a laminar process ventral to the inferior setae.

Etymology. The specific epithet is a Latin noun in apposition meaning "promontory", alluding to the geographic setting of the type locality.

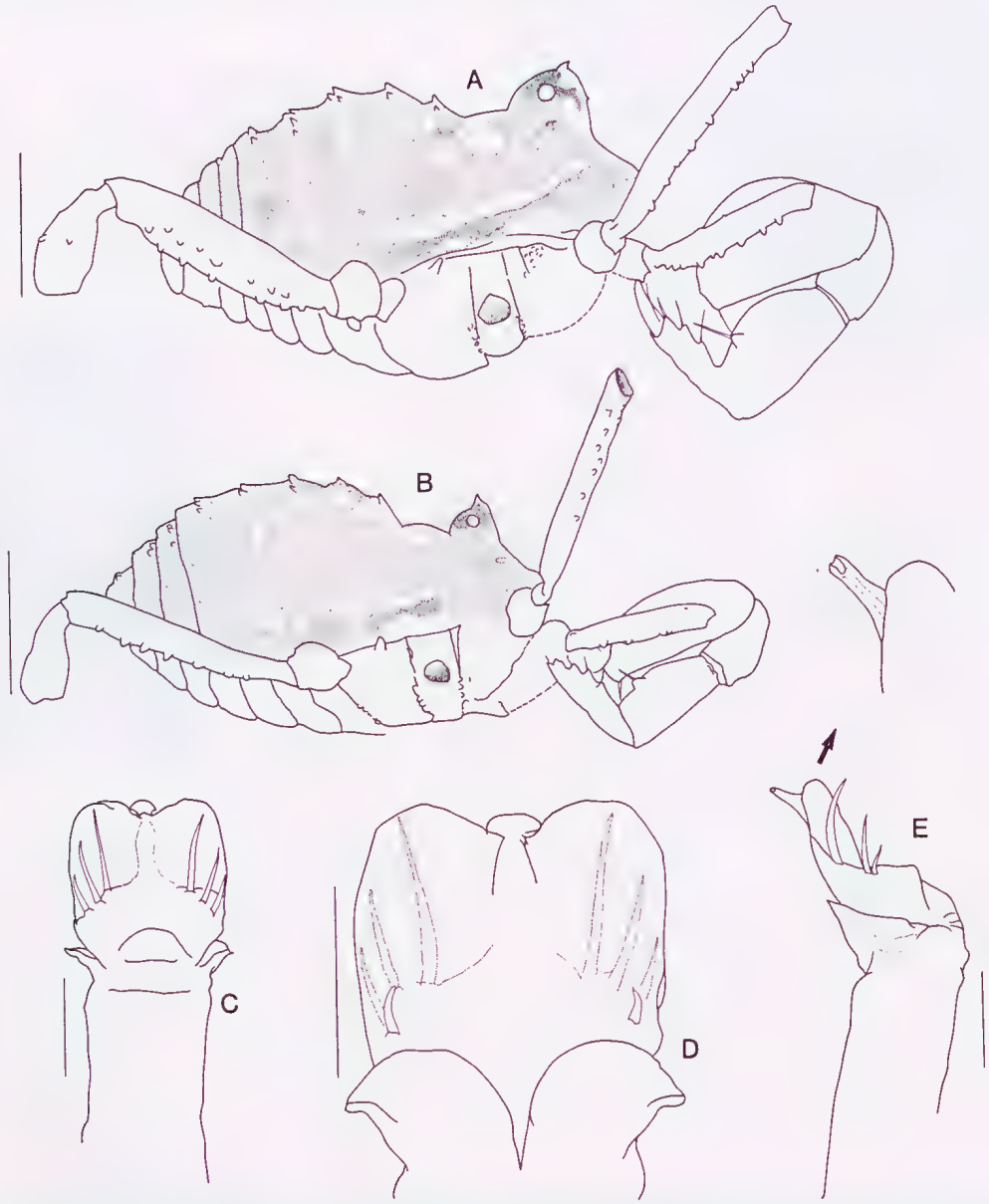

Fig.14. *Lomanella kallista* Forster. A,C-E = male KS23226; B = female KS23226. A-D = body, lateral; C,D = terminal part of penis, ventral, dorsal and lateral with detail. Scale bars: A,B = 1 mm; C-E = 0.1 mm.

Distribution. Victoria: Wilsons Promontory.

Lomanella insolentia species group

South-east Australia and Tasmania; claw of tarsi III and IV with pair of lateral branches forming an angle with central prong and with scale like branch at base of each lateral branch; penis with stylus extending beyond sensillar region by at least 0.3 sensillar carrier length; sensillar region with lateral wing-like processes; tarsus II with 5 articles.

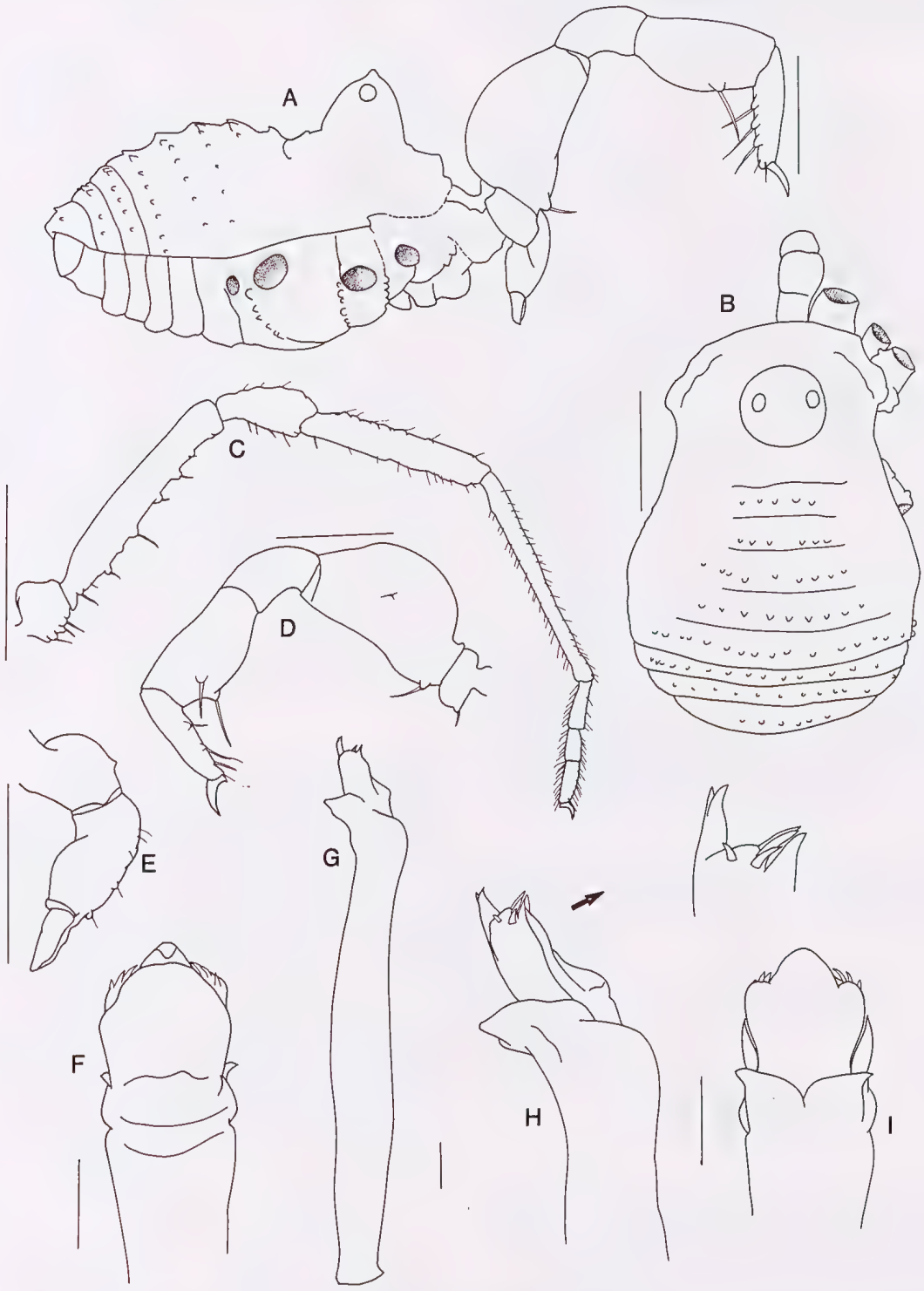

Fig.15. *Lomanella promontorium* n.sp. A-I = holotype male. A = body and pedipalp, lateral; B = dorsum; C = right leg I, retrolateral; D = pedipalp, prolateral; E = chelicera, lateral; F-I = penis, ventral, entire penis (lateral), lateral with detail and dorsal. Scale bars: A-E = 1 mm; F-I = 0.1 mm

Lomanella insolentia n.sp.

Figs 6,16

Type material. New South Wales: HOLOTYPE male, KS23218, Tom Groggin, Kosciusko National Park, 36°33'S 148°09'E under logs, wet sclerophyll, G.S. Hunt, 2 Jan. 1970. PARATYPES: KS23219, same data, 1 female; KS23220, same data, 1 male, 1 female; KS23221, Lakeside Inn area, Kosciusko National Park, under log, snow gum woodland, G.S. Hunt, 1 Jan. 1970, 1 female. Victoria: KS23222, Bogong High Plains, under log, snow gum woodland, G.S. Hunt, 3 Jan. 1970; MOV K-1033, Errinunda Plateau, Errinunda Road, soil/litter sample, Tullgren extraction, *Eucalyptus fastigata* plantation, A.L. Yen, 15 Mar. 1982.

Other material examined. New South Wales: KS23223,

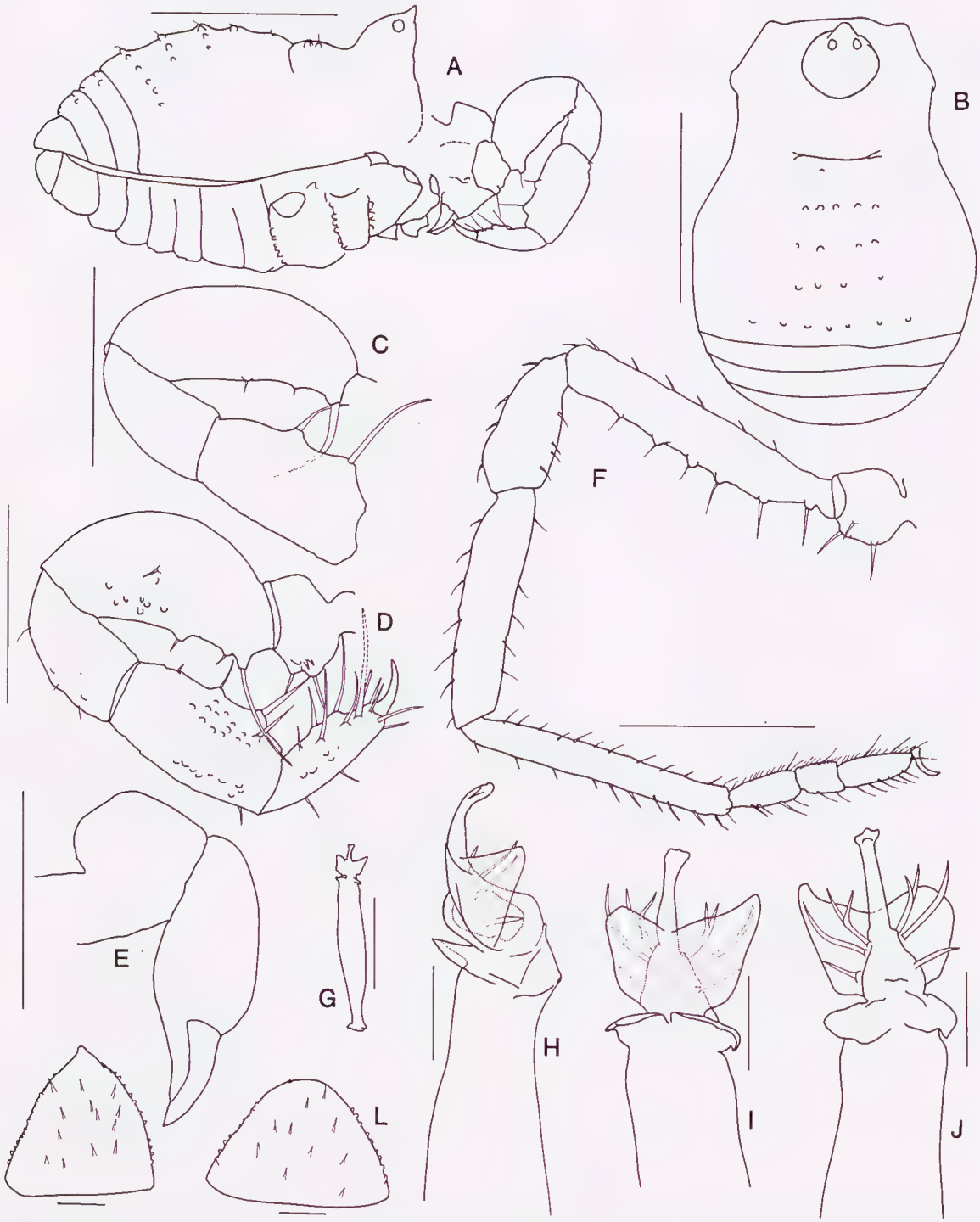

Fig.16. *Lomanella insolentia* n.sp. A,B,D-K = male KS23220; C,L = female. A = body and pedipalp, lateral; B = dorsum; C,D = pedipalp, retro- and prolateral; E = chelicera, lateral; F = right leg I, retrolateral; G-J = penis, entire (ventral), lateral, dorsal and ventral; K,L = genital operculum. Scale bars: A,B = 1 mm; C-G = 0.5 mm; H-L = 0.1 mm.

Little Peppercorn Hill, Bridabella to Rules Point Road, Kosciusko National Park, G.S. Hunt, 28 Dec. 1969, 1 male.

Diagnosis. SL about 2 mm, eyemound rising vertically immediately behind anterior margin, with small apical spine; sensillar region of penis each side with broad wing-like lamina, setae inserted towards midline.

Description. MALE. *Body:* small, SL 1.81-2.10 (1.95, 3), CW 1.13-1.24 (1.19); dorsal pigmentation pattern faded in preservation; eyemound rising almost vertically immediately behind anterior margin, armed with a small apical spine, more rounded posterior to spine. Carapace posterior to eyes with mesial granules (Fig.6D). Scutal groove moderately deep; TA1-5 defined by mesial grooves, each TA and free tergite with row of small setose granules; otherwise dorsum evenly granulate; genital operculum triangular and pointed at apex. *Pedipalps:* PFL 0.65-0.73 (0.69); size of setal bases are as follows (compare with Fig.1): fv1, fv2, fv4, fpl1 weak, trv2, trv3, tpv2 weak, tpv1 lacking, tarsus as figured; seta of trv3 smaller than seta of fv1. *Legs:* FIV 1.12-1.23 (1.17); femora tuberculate ventrally; claw of tarsus IV with a small scale-like lateral prong at the base of each lateral prong, TF 3(2),5(3),4,4. *Penis:* sensillar region of penis clearly differentiated from stylus, in ventral view composed of a central area bearing 4 pairs of setae, and lateral wing-like laminae apparently homologous to ventral plate.

FEMALE. Similar to male except: pedipalp less robust, genital operculum broader at base and rounded apically (Fig. 16L); ovipositor with unevenly bifid setae fringing vaginal opening. Key measurements: SL 1.97, CW 1.14, PFL 0.61, FIV 1.10.

Variation. Pedipalp spine trv2 lacking in some specimens. The single male from Little Peppercorn Hill (KS23223) is at the northern limit of the known species range. The eyemound is similar and the penis of the same general form except that the lateral wing-like processes are not as extended distad and the setae are relatively shorter. The pedipalp femur lacks fv4 and the tibia lacks tpv2. Despite these differences, this specimen is tentatively assigned to *L. insolentia.*

Comments. This species is very close to *L. troglophilia* which it resembles in the general form of the eyemound, the claw of tarsus IV, and tibial spination. It evidently is also close to *L. revelata* but in the latter species the ventral plate is fully differentiated from the stylus mesially as well as laterally.

Etymology. The specific epithet is a Latin noun in apposition meaning "arrogance" and refers to the haughty nature of the high eyemound topped with a short curved spine.

Distribution. South-east New South Wales and north-east Victoria, "Australian Alps" region.

Lomanella revelata n.sp.

Fig.17

Type material. New South Wales: HOLOTYPE male, ANIC, Fern Glen, 3 km south of Bundanoon, rainforest 650 m, ANIC berlesate no. 139, Britton & Upton, 6 May 1969. PARATYPES: Clyde Mountain, rainforest, 800 m: ANIC berlesate no. 469, R.J. Kohout, 15 Jul. 1973, 1F; ANIC berlesate no. 2, leafmould, R.W. Taylor, 24 Dec. 1966, 1F.

Diagnosis. SL between about 1.3 and 1.6 mm, eyemound armed with a short tubercle, anteriolateral corner of carapace with small tubercle, penis with fully expressed ventral plate.

Description. MALE. Similar to *L. insolentia* except: body smaller, SL 1.43, CW 0.93; dorsal pigmentation pattern as figured, eyemound rising steeply about 0.5 IOD behind anterior margin, anterior margin with a small tubercle inside each corner; dorsal mound on cheliceral first segment slightly coriaceous; PFL 0.54; pedipalp with fv4 and trv2 lacking; FIV 0.88; lateral laminae of sensillar region meet midventrally resulting in a fully expressed ventral plate clearly differentiated from the stylus in lateral view (Fig.17I).

FEMALE. Similar to male. Key measurements: SL 1.44, CW 0.79, PFL 0.49, FIV 0.89.

Comments. This is the most northerly known species of *Lomanella.* The penis is of the general form with a fully developed ventral plate discussed by Martens (1986: fig.2b) (see also our Fig.3 and discussion above). The disposition of setae on the penis and general body form indicate that this species is most closely related to *L. insolentia* despite the fact that the latter does not have a fully expressed ventral plate.

Etymology. The specific epithet is a past participle of the Latin verb "to reveal" and refers to the role of the animal's penis in revealing phylogenetic trends in *Lomanella.*

Distribution. New South Wales: Bundanoon to Clyde Mountain area.

Lomanella troglophilia n.sp.

Figs 6,7,18

Type material. Tasmania: HOLOTYPE male: KS23247, Kutikina Cave (F34), Franklin River, 42°30'S 145°45'E, on dry substrate in deep threshold zone, S. Eberhard, 23 Mar, 1988. PARATYPES: KS23249, same data, 2 males; KS23248, same data, 5 females; KS23250, Kutikina Cave, dark zone and twilight zone, S. Eberhard, 21 Mar. 1989, 2 males; KS23251, Kutikina Cave, End Chamber, S. Eberhard, 21 Mar. 1989, female.

Other material examined. Tasmania: KS24854, Gordon River, transect 10R213, HEC Survey, under log, J.L.H. & P.J.S., 3 Feb. 1976, male; KS23253, Bubs Hill, Minimoria Cave (BH-202), caught in drift net in flood, dark zone, S. Eberhard, 31 Dec. 1986, male; KS23254, Bubs Hill, Cave BH-16, A. Clarke, 9 Mar. 1988, KS23255, Bubs Hill, Cave BH-13, dark zone, A. Clarke, 9 Mar. 1988, female; KS23256, Andrew River, "Cave No.1", S. Eberhard, 23 Mar. 1988, female; KS23252, Nicholls Range, 42°40'S 145°50'E, Bill Nielsen Cave (NR-1), S. Eberhard, 19 Feb. 1987; KS 23259, Mount Cripps, 41°35'S 145°46'E, Philrod Cave (CR-3), S. Eberhard, 1990, male, 2 females.

Fig.17. *Lomanella revelata* n.sp. Holotype male. A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C = chelicera and eyemound, lateral; D = right leg I, retrolateral; E = pedipalp, retrolateral; F = claw IV, retrolateral; G-J = penis, entire (ventral), ventral, lateral and dorsal. Scale bars: A-E = 0.5 mm; F-J = 0.1 mm.

Diagnosis. Frequently cavernicolous, eyemound with spine and rising at about 45° well behind anterior margin, TA1-5 delineated by deep grooves, dorsum mostly dark brown, pedipalp femur with fv4 present, tibia with 3 setose tubercles, namely trv2, trv3 and tpv2, lateral wing-like lobes of sensillar region with predominantly dorsoventral orientation.

Description. MALE. Similar to *L. insolentia* except: body smaller, SL 1.72-1.84 (1.78, 4), CW 0.98-1.06 (1.03); pigmentation pattern of dorsum as figured; eyemound rising at about 45° about 1.0 IOD behind

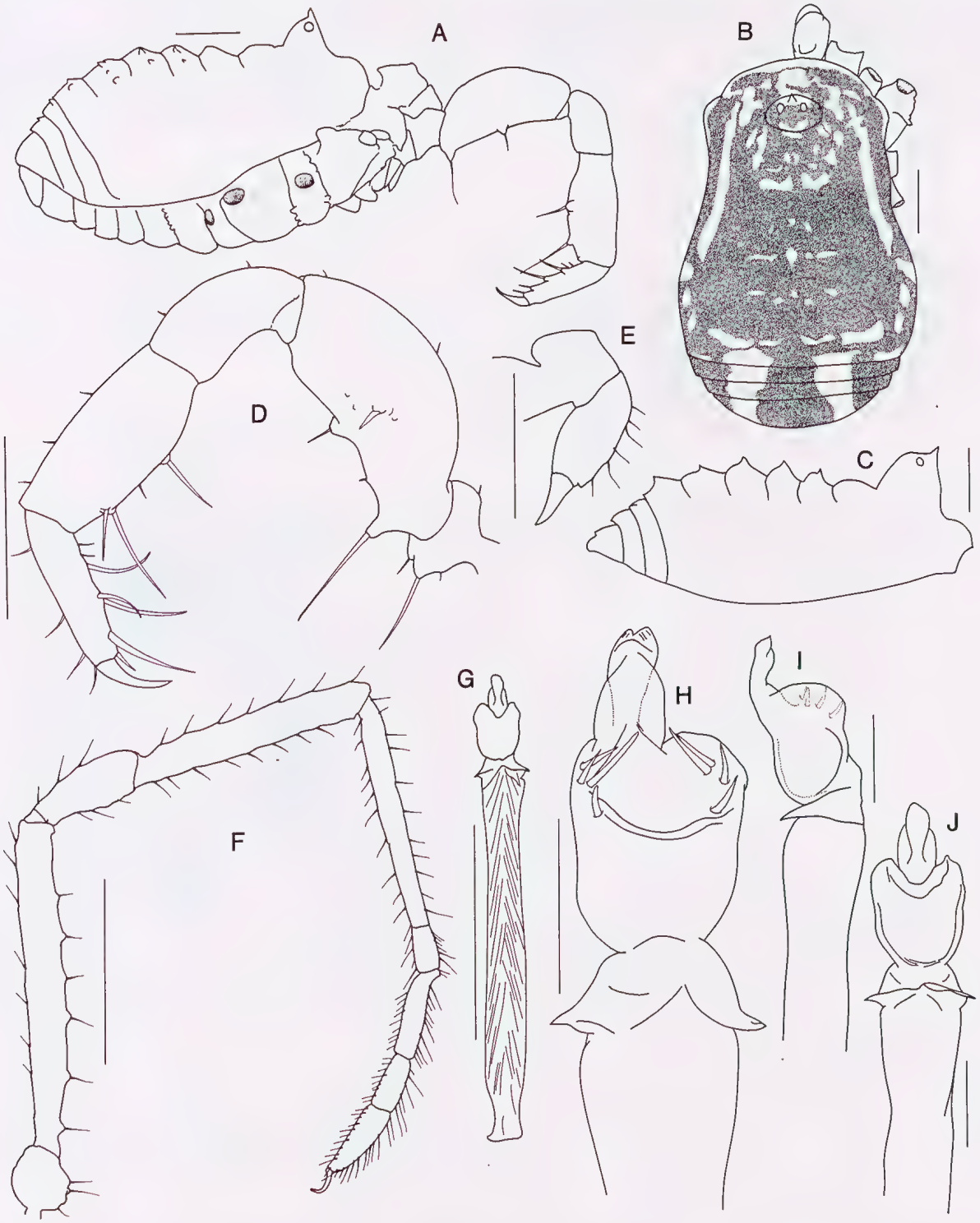

Fig.18. *Lomanella troglophilia* n.sp. A,B, D-J = male *ex* Kutikina Cave; C = male KS24854 *ex* surface, Gordon River. A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C = scute, lateral; D = pedipalp, prolateral; E = chelicera, lateral; F = right leg I, retrolateral; G-J = penis, entire (ventral) showing muscle in truncus, ventral, lateral and dorsal. Scale bars: A-G = 0.5 mm; H-J = 0.1 mm.

anterior margin; carapace with mesial groove at posterior margin of eyemound, followed by mesial hump which is slightly depressed at its midline (Fig.6H); scutal groove deep, TA1-5 delineated mesially by deep grooves, each TA with rows of strong setose granules; PFL 0.72-0.78 (0.76); legs elongate in cave specimens, FIV 1.33-1.44 (1.39); TF 3(2),5(3),4,4; sensillar region concave ventral to stylus but laterally with raised lobes with strong ventrodorsal orientation bearing 4 setae, lobes apparently homologous to ventral plate, at least its lateral sectors; dorsolateral plate in lateral view orientated perpendicular to axis of penis.

FEMALE. Similar to male except: pedipalps slightly less robust, genital operculum wider at base. Key measurements: SL 1.87, CW 1.03, PFL 0.73, FIV 1.32.

Variation. Specimens from Bill Nielson Cave, Nicholls Range, have yellow pedipalps with no clear trace of pigmented reticulations present in other populations. Mean measurements for 4 males from Bubs Hill Caves are: SL 1.66, CW 0.99, PFL 0.75, FIV 1.42. The surface specimen from the Gordon

Fig.19. *Lomanella alata* n.sp. Holotype male. A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C = pedipalp, retrolateral; D = right femur and patella I, retrolateral; E-G = penis, lateral, dorsal and ventral. Scale bars: A,B = 1 mm; C,D = 0.5 mm; E,F = 0.1 mm.

River area has a larger and higher eyemound and very deep grooves between the tergal areas.

Comments. Penis in lateral view very similar to that in *L. alata*. The legs of cave specimens are somewhat elongate but the dorsum remains heavily pigmented.

Natural history. Cave specimens were frequently observed in pairs on dry walls and dry silt floors (S. Eberhard, label note). The species appears to be rare on the surface.

Etymology. The specific epithet refers to tendency for this animal to live in caves, 'troglophile' being a facultative cavernicole which may spend some or all of its life cycle in caves, but can also live on the surface.

Distribution. Known from south-west Tasmania, and Mount Cripps, central northern Tasmania.

Lomanella alata n.sp.

Fig.19

Type material. Tasmania: HOLOTYPE male: KS23146, Transect 2L.1140, south-west Tasmania, 42°43'S 145°49'E, moss, L. Hill & party, 16 Feb. 1978.

Diagnosis. Eyemound rising immediately behind anterior margin, without spine; dorsum with a large yellow mesial patch, TA1-5 not separated by deep grooves; sensillar region in ventral view with a distolateral wing-like expansion on each side which carries the setae.

Description. MALE. Similar to *L. insolentia* except: SL 1.49, CW 0.91; dorsal pigmentation pattern as figured, dorsum predominantly yellow with mesial area flanked by irregular stripes of dark brown pigmentation which tend to meet posteriorly in TA5; PFL 0.54, PFL:CW 0.59, fv4 and trv2 lacking; FIV 0.81, FIV:CW 0.89, claw of leg IV not examined; sensillar region of penis narrow basally and expanding distally into large wing-like lobes each group of 4 setae, lobes apparently homologous to ventral plate, at least its lateral sectors.
FEMALE. Unknown.

Comments. This species is very close to *L. troglophilia* in genital morphology but differs in several external characters including pigmentation pattern, lack of a spine on the eyemound and spination of pedipalp tibia.

Etymology. The specific epithet refers to the wing-like lobes seen in ventral view on the sensillar region of the penis.

Distribution. South-west Tasmania.

Lomanella exigua species group

South-eastern Australia, especially Tasmania; claw of tarsi III and IV a peltonynchium; tarsus I with 2-3 articles, tarsus II with 3-5 articles; sensillar region with same axis as penis truncus (when penis not expanded); sensillar region extending as a narrow mesial process beyond level of setae and lying against the stylus.

Lomanella exigua V.V. Hickman

Figs 6,20

Lomanella exigua V.V. Hickman, 1958: 15-16.

Type material. South-east Tasmania: HOLOTYPE male: KS6919, Arve Forest, Geevestown, 43°10'S 146°55'E, V.V. Hickman, 1 Dec. 1955. ALLOTYPE female: KS17865, same data.

Other material examined. South-east Tasmania, Arve Forest: KS24243, J.L. & V.V. Hickman, 11 Dec. 1955, 3 males, six females; KS24244, J.L. & V.V. Hickman, 22 Nov. 1955, 3 males, 1 female.

Diagnosis. Dorsum brown-orange, eyemound rounded, without spine, anteriolateral corner of carapace with forward projection, TA1-5 and free tergites without rows of granules/tubercles, claw of

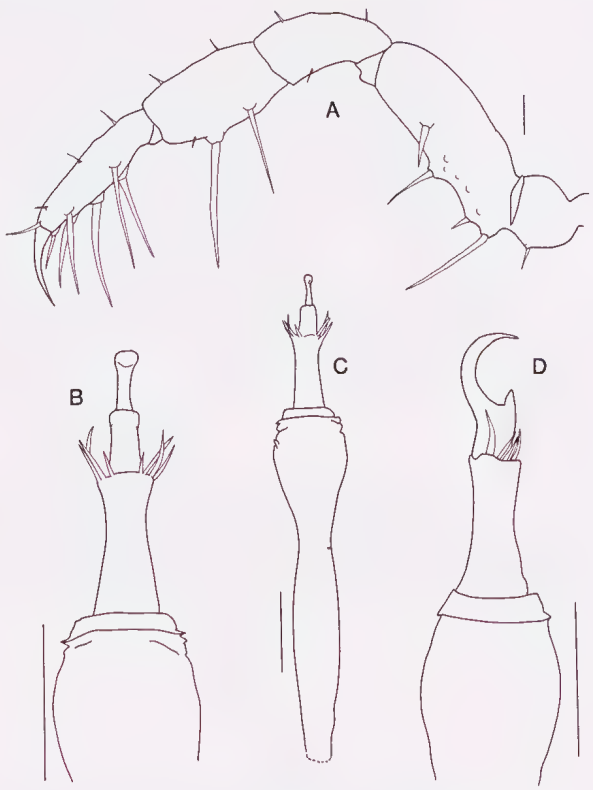

Fig.20. *Lomanella exigua* Hickman. Male KS24244. A = pedipalp, prolateral; B-D = penis, ventral, entire (ventral) and lateral. Scale bars: A-D = 0.1 mm.

tarsus IV a complex peltonychium, shaft of penis very broad distally, broader than sensillar region, distal extension of sensillar region with flat termination in ventral view.

Redescription. MALE. *Body:* small, SL 1.48-1.53 (1.52, 6); CW 0.90-0.94 (0.92). Pigmentation pattern as figured by V.V. Hickman (1958) and similar to that of *L. browni* n.sp. (Fig.21B), dorsum brown-orange relieved by yellow patches including a stripe down each flank and a mesial area posteriorly. Eyemound rounded and smooth except for normal but large surface granules (Fig.6I), rising about 1.0 IOD from anterior margin; carapace with an angular projection in each anteriolateral corner; scutal groove distinct mesially, TA1-5 separated by shallow depressions in which some surface granulation occurs; TA themselves with areas devoid of surface granules, particularly TA 3-5; free tergites also smooth (Fig.6C); genital operculum triangular. *Pedipalps:* PFL 0.52-0.55 (0.54); yellowish with brown reticulations; fv1, fv4 and fpl1 moderately developed, fv2 small, trv2 and tpv2 lacking (unless tpv2 has migrated to position of tpv1), trv3 larger than fv1, tarv2 slightly larger than tarv1, tarsus with 3 proventral and 4 retroventral setose tubercles. *Legs:* FIV 0.76-0.81 (0.79); ventral surface of femur I with weak development of setose tubercles in proximal half; tarsal claw of legs III and IV in form of a peltonychium (see Fig.7G for claw of related species) with about 12 scale-like accessory branches on each side; TF 3(2),3(2),4,4. *Penis:* truncus very swollen distally and terminates at a rim which may be homologous to the dorsolateral plate, sensillar region elongate and carries subdistally 4 setae on each side (V.V. Hickman mentions 2); sensillar region extends distoventrally beyond setae, terminating bluntly in ventral view, in lateral view terminating sharply (this structure apparently homologous to ventral plate); stylus sickle shaped in lateral view.

FEMALE. Similar to male, pedipalps slightly more slender, genital operculum wider at base. Key measurements: SL 1.43, CW 0.87, PFL 0.50, FIV 0.75.

Variation. V.V. Hickman (1958) records one female with tarsal formula 2,2,4,4.

Comments. *Lomanella exigua* is very difficult to distinguish on external characters from another surface species, *L. browni* n.sp., but is readily distinguishable on genital morphology. It appears to have a much more restricted distribution than the latter species.

Distribution. Tasmania: Geeveston area.

Lomanella browni n.sp.

Figs 7,21

Type material. South Tasmania: HOLOTYPE male: KS24899, Huon River, 43°06'S 146°44'E, wet sclerophyll, Australian Biological Resources Study Survey vial 2964, J.L. Hickman *et al.*, 29 May 1974. PARATYPES: Australian Biological Resources Study Survey, southern Tasmania: KS24898, wet sclerophyll, vial 3053, J.L. Hickman *et al.*, 29 May 1974, male; 43°05'S 146°44'E, wet sclerophyll, J.L. Hickman *et al.*, 20 May 1974, male; Hydro-Electricity Commission South-west Tasmania Survey: KS24855, 42°31'S 145°46'E, mixed rainforest, transect 3R 10, L. Hill & party, 9 Jan. 1978, female; KS24874, 42°34'S 145°43'E, moss, open forest, transect 10R 1055, C. Howard *et al.*, 2 Feb 1976, female; TMAG, J3031, same data, female; KS24856, 42°31'S 145°45'E, Transect 3R 1300, C.L. Howard, 8 Feb. 1977, F; KS24857, 42°43'S 145°49'E, scrub rainforest, transect 2R 70, C.J. Howard & party, 8 Feb. 1977, female; KS24858, 42°41'S 145°54'E, wet scrub, moss transect 4.2200, C. Howard & party, 14 Feb. 1977, male; KS24859, 42°48'S 145°51'E, wet scrub, transect 5R 400, L. Hill & party, 4 Mar. 1977, female; KS24860, 42°41'S 145°48'E, scrub rainforest, transect 1L 50, female; KS24872, 43°05'S 146°44'E, wet sclerophyll, vial 3012, J.L. Hickman & party, 20 May 1974, male.

Diagnosis. Dorsum brown-orange, eyemound rounded, without spine, anteriolateral corner of carapace with forward projection, TA1-5 and free tergites without rows of granules/tubercles, claw of tarsus IV a complex peltonychium, truncus of penis not very broad distally, narrower than sensillar region, distal extension of sensillar region with mesial terminal V-shaped notch in ventral view.

Description. MALE. Very similar to *L. exigua* except: SL 1.57-1.61 (1.58, 3); CW 0.93-0.94 (0.94); PFL 0.52-0.56 (0.54); FIV 0.80-0.81 (0.81); shaft of penis not swollen distally, separated from sensillar region by two broad flanges which are presumed homologous to dorsolateral plate; sensillar region broader than distal end of truncus and carrying a group of 3 inferior setae towards each distolateral corner and a superior seta placed dorsally, distal extension of sensillar region with terminal V-shaped notch.

FEMALE. Differs from male as in *L. exigua*. Key measurements SL 1.62, CW 0.94, PFL 0.55, FIV 0.80.

Comments. The penis of this species seems more plesiomorphic in form than that of *L. exigua*. The arrangement of setae into a clearly identifiable superior seta and group of inferior setae is closer to that of other Australian Triaenonychidae.

Etymology. The specific epithet is in recognition of the work of Dr Bob Brown, Member of the Parliament of Tasmania, in leading the effort to secure World Heritage status for south-west Tasmania, the region in which this species occurs.

Distribution. South-west and southern Tasmania.

Lomanella parva Forster

Lomanella parva Forster, 1955: 390-392.–V.V. Hickman, 1958: 15.

Type material. Tasmania: HOLOTYPE male: QM, no. W1897, Wallaby Beach, Port Davey, ex leafmould, E.N. Marks, 29 Jan. 1954 (genitalia on slide). ALLOTYPE female: QM, no. W1898, same data.

Comments. Both types have been subject to desiccation and fungal attack, and the holotype has also suffered mechanical damage. As there is no further material available, the species is not redescribed here. The permanent mount of the penis clearly shows the four pairs of long setae illustrated by

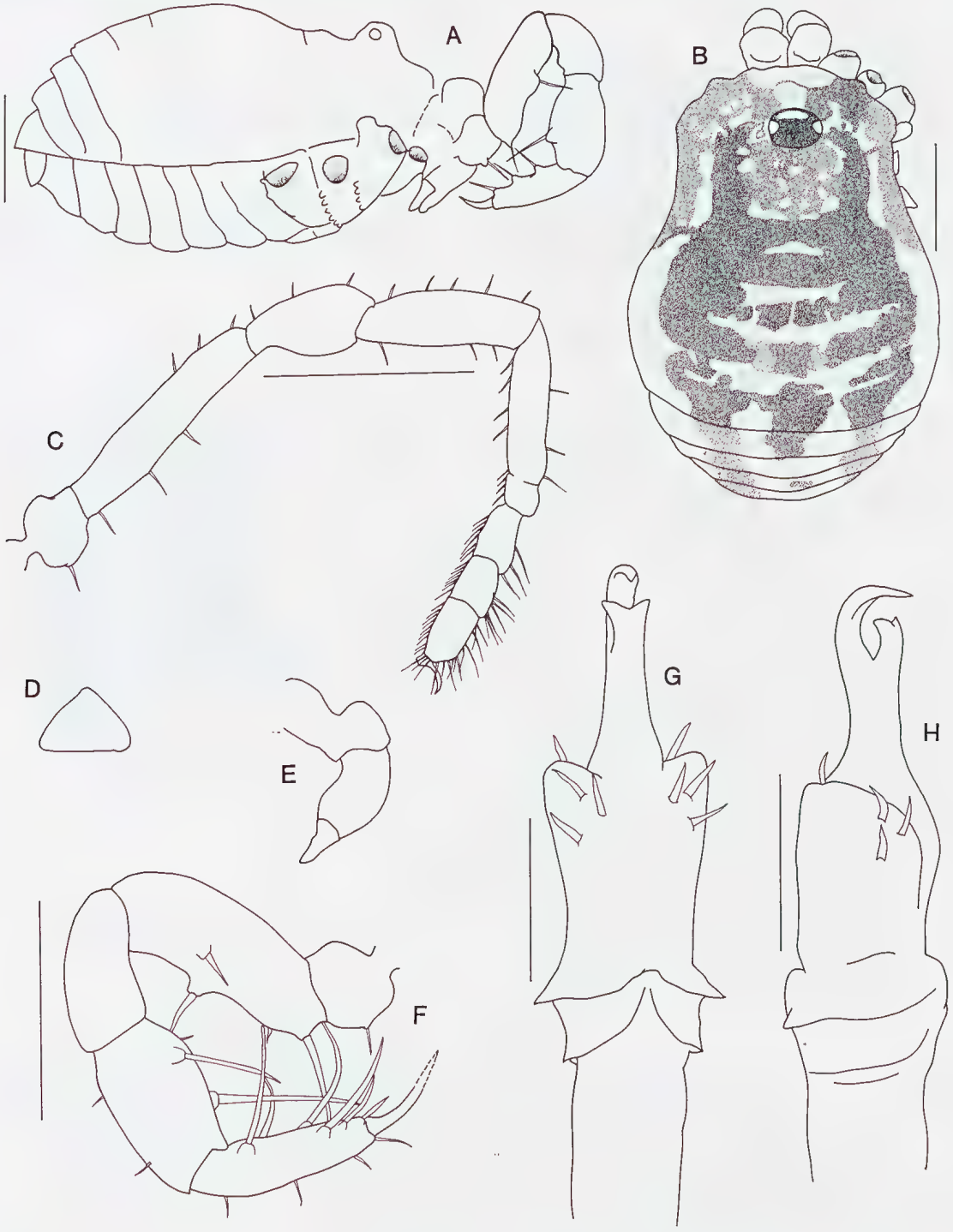

Fig.21. *Lomanella browni* n.sp. A-F = male KS19750. A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C = right leg I, retrolateral; D = genital operculum; E = chelicera, lateral; F = pedipalp, prolateral; G,H = penis, ventral and lateral. Scale bars: A-C,F = 0.5 mm; G,H = 0.1 mm. D,E same scale as F.

Forster. The species is very close to *L. quasiparva*, differing in details of penis morphology and pedipalp spination.

Distribution. South-west Tasmania: Port Davey.

Lomanella quasiparva n.sp.

Figs 8,22

Type material. South-west Tasmania: HOLOTYPE male: KS20035, 42°37'S 145°45'E, in moss, *Eucalyptus nitida* woodland, C. Howard & party, 5 Feb. 1976. PARATYPES: South-west Tasmania Hydroelectricity Commission Survey: KS23145, 42°34'S 145°43'E, moss, open forest, C. Howard & party, 2 Feb. 1976, female. KS24862, 42°43'S 145°50'E, moss, wet scrub, C. Howard & party, 8 Feb. 1977, female; KS24863, 42°41'S 145°53'E, scrub rainforest, C. Howard & party, 14 Feb. 1977, female; KS24864, 42°41'S 145°52'E, scrub rainforest, C. Howard & party, 14 Feb. 1977, female; KS24865, 42°41'S 145°53'E, wet scrub, C. Howard & party, 14 Feb. 1977, female; KS24866, Strathgordon, 42°46'S 146°03'E, moss on log, J.L. Hickman, 16 May 1978, female; TMAG, J3030, same data, male, female; KS24867, Strathgordon, moss, *Nothofagus* - *Eucalyptus* forest, J.L. Hickman, 25 Apr. 1978, male; KS24868, 42°41'S 145°53'E, moss, scrub rainforest, C. Howard & party, 14 Feb. 1977, female; KS24869, same data, female; KS24870, 42°51'S 145°50'E, moss, closed forest, C. Howard & party, 18 Feb. 1976, male; KS24871, 42°35'S 145°43'E, closed forest, C. Howard & party, 28 Jan. 1976, female.

Diagnosis. Body yellow brown; tarsus I and II of male with 2 articles, penis with 3 setae, most ventral one short.

Description. MALE. Similar to *L. exigua* except: body smaller, SL 1.15-1.23 (1.20, 5), CW 0.75-0.77 (0.76); colour yellow with dark brown pigmentation as figured; eyemound rising about 0.5 IOD, posterior

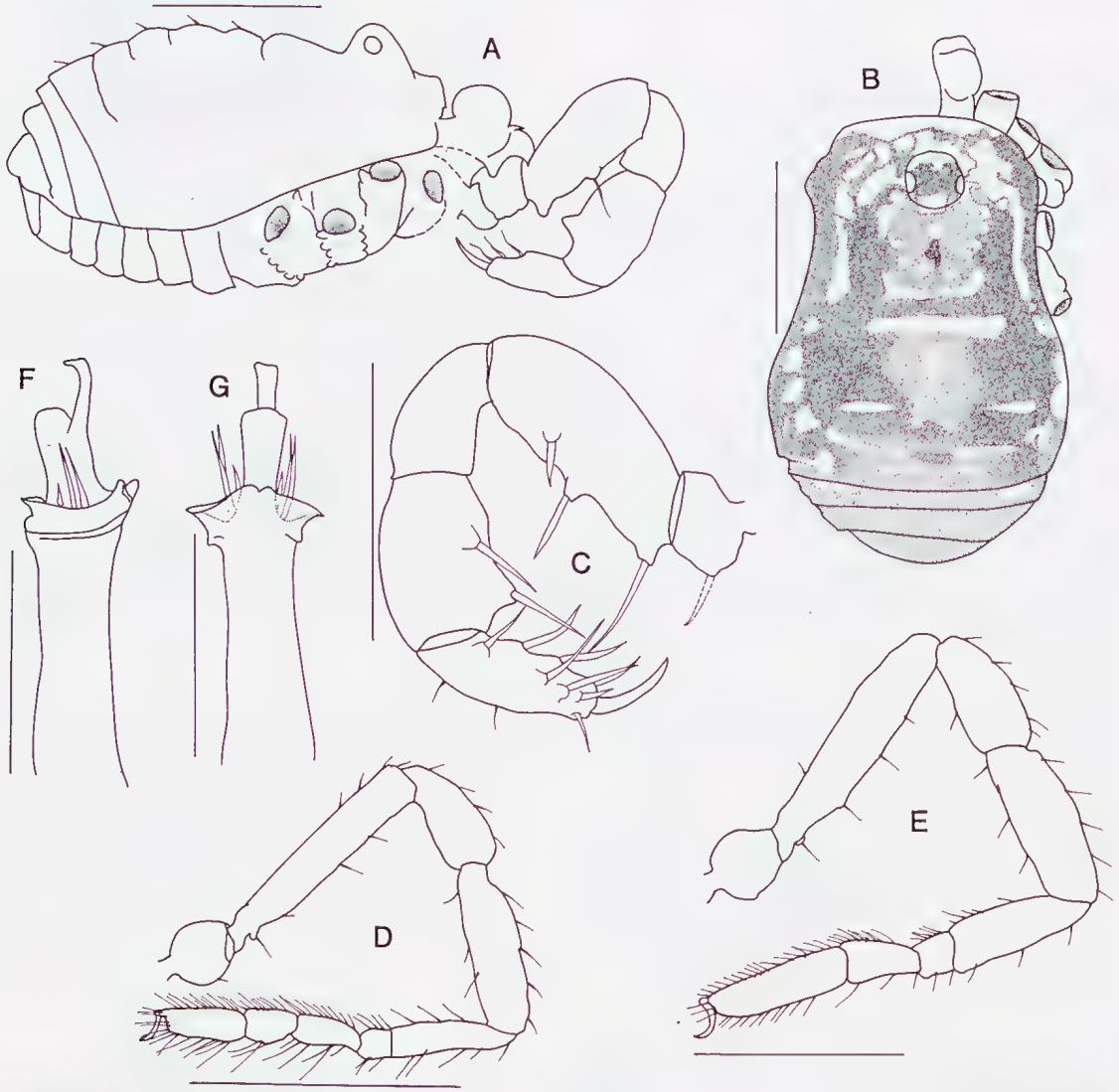

Fig.22. *Lomanella quasiparva* n.sp. A-C,E-G = male KS20035; D = female. A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C = pedipalp, prolateral; D,E = right leg I, retrolateral; F,G = penis, lateral and ventral. Scale bars: A-E = 0.5 mm; F,G = 0.1 mm.

slope steeper than anterior; process in anteriolateral corners of carapace lacking; tergal areas and free tergites granulate, TA1-5 each with row of tiny setose granules; PFL 0.42-0.46 (0.44); pedipalp with fv2 lacking, fv4 strong, trv3 very strong; FIV 0.61-0.66 (0.65); claw of tarsus IV slightly less complex with about 8 lateral branches on each side of the central prong; leg femora without ventral tubercles, TF 2(1),2(1),4,4; truncus of penis not swollen distally, terminating in dorsolateral plate which forms virtually continuous rim around penis (Fig.8D) and lies at level of the setae, sensillar region not elongate proximal to setae; distal extension of sensillar region blunt in lateral view, most ventral seta on each side very short, about 0.5 length of the 2 setae lying more dorsally.

FEMALE. Similar to male except: pedipalp less robust, genital operculum wider at base, TF 3(2),3(2),4,4. Key measurements: SL 1.22, CW 0.75, PFL 0.40, FIV 0.62.

Comments. *Lomanella quasiparva* shares with *L. parva* only two articles in tarsus I and II of the male. This condition resembles the last instar of other species where there is subdivision of the tarsus into pro- and distitarsus but not subdivision of the distitarsus into two or more articles. Hence the condition in the male may be an example of neoteny where a juvenile character is retained in the adult.

We considered whether this synapomorphy indicated that *L. quasiparva* and *L. parva* are conspecific. We believe, however, that the difference in size and number of penile setae warrants separate species status. The form of the penis also appears to differ though this may be an artifact due to mounting or to variation in the state of penis expansion.

Etymology. The specific epithet means simulating *parva*.

Distribution. South-west Tasmania.

Lomanella thereseae n.sp.

Figs 6,7,23,24

Type material. South-east Tasmania, King George V Cave, Hastings, 43°23'S 146°51'E: HOLOTYPE male: KS23267, underside of charcoal wood debris, A. Clarke, 21 Oct. 1988. PARATYPES: KS23240, A Goede, 30 June 1974, male; KS23242, A. Goede & J. Richardson, 30 June 1974, 2 males; KS23244, T. Goede, 21 Oct. 1971, female; KS17251, T. Goede, 17 July 1971, female; KS23245, T. Goede, 2 Nov. 1975, 2 females; A. Goede & G.S. Hunt, Oct. 1982, 3 males, 4 females; KS23266, underside of charcoal wood debris, A. Clarke, 21 Oct. 1988, male.

Other material examined. Tasmania: Ida Bay caves, 43°30'S 146°50'E: KS21468, Mystery Creek Cave, T. Goede, 4 Feb. 1976, male, female; KS21470, Mystery Creek Cave, T. Goede, 15 Nov. 1975, female; KS23268, Cave IB91, S. Eberhard, male; KS23269, Cave IB14, S. Eberhard, 1990, male; KS23241 Cave IB4, S. Eberhard, 1990, male. Weld River Arch Cave, 42°50'S 146°25'E: KS23260, threshold zone, S. Eberhard, 11 May 1986.

Diagnosis. Often cavernicolous, body orange-yellow with little or no pigmentation, pedipalp tibia with 4 setose tubercles, namely trv2, trv3, tpvi and tpv2.

Description. MALE. Similar to *L. exigua* except: SL 1.58-1.63 (2), CW 0.97-0.99; body with only traces of pigmentation, overall colour orange-yellow; eyemound lower in profile, eyes reduced in size, process in anteriolateral corners lacking, tergal areas and free tergites granulate, TA1-5 defined by prominent grooves, each TA carrying a row of setose granules; pedipalp relatively longer, PFL 0.72-0.7; fv2 larger, fv4 smaller (almost lacking in Ida Bay Caves populations); tibia with 4 setose tubercles, trv2, trv3, tpv1, tpv2; trv3 relatively much larger than fv1; legs relatively much more elongate, FIV 1.27-1.31; claw of tarsus IV much less complex with only about 4 lateral branches on each side of the central prong (Fig.7D); TF 3(2),5(3),4,4; truncus of penis not swollen distally, dorsolateral plate well defined and lying immediately proximal to setae, sensillar region not elongate proximal to setae; distance between dorsolateral plate and more proximal flange much greater; distal extension of sensillar region larger and blunter in lateral view, stylus less sickle-shaped.

FEMALE. Differs from male as in *L. exigua*. Key measurements SL 1.68, CW 0.97, PFL 0.73, FIV 1.25.

Variation. There is some variation in eyemound size, one specimen from Ida Bay caves having a very low eyemound (Fig.6J). Ida Bay specimens essentially lack fv4 which is indicative of genetic isolation from the Hastings Cave population as electrophoretic studies seemed to show for the respective populations of *Hickmanoxyomma cavaticum* (Hunt, 1990). Mean measurements for three Ida Bay cave males are: SL 1.50, CW 0.91, PFL 0.67, FIV 1.16, PFL:CW 0.74, FIV:CW 1.27. Measurements for Weld River Arch male: SL 1.58, CW 0.93, PFL 0.74, FIV 1.40, PFL:CW 0.80, FIV:CW 1.51. A male specimen from the surface at Arve Valley is SL 1.57, CW 0.96, PFL 0.67, FIV 1.30, PFL:CW 0.72, FIV:CW 1.35.

Comments. Contrary to earlier views, for example in Eberhard (1990), the species as recognised here is not a strict troglobite. Specimens from the surface in the Arve Valley, an area without caves, have depigmentation and relative appendage length comparable to the cave specimens. *Lomanella thereseae* is much less troglomorphic than the other cavernicolous member of the species group, namely *L. troglodytes*, which is completely blind and has relatively much longer legs. Nevertheless, it is possible that one or more of the cave populations may be troglobitic - no surface specimens

have been found at Ida Bay and Hastings despite repeated collecting, and variation between these populations (noted above) suggests restricted gene flow. Electrophoresis might demonstrate that *L. thereseae* consists of two or more cryptic species.

The single male specimen from Weld River Caves had a deep ventral concavity in the penis (Fig.24F). As the concavity is regular in shape, we have assumed that it is neither an artifact nor a deformity. However, the specimen appears identical in other respects to the Hastings Cave population except in having longer appendages, so we have conservatively placed it in *L. thereseae* pending further material. Spination of the pedipalp tibia is the most plesiomorphic for *Lomanella*,

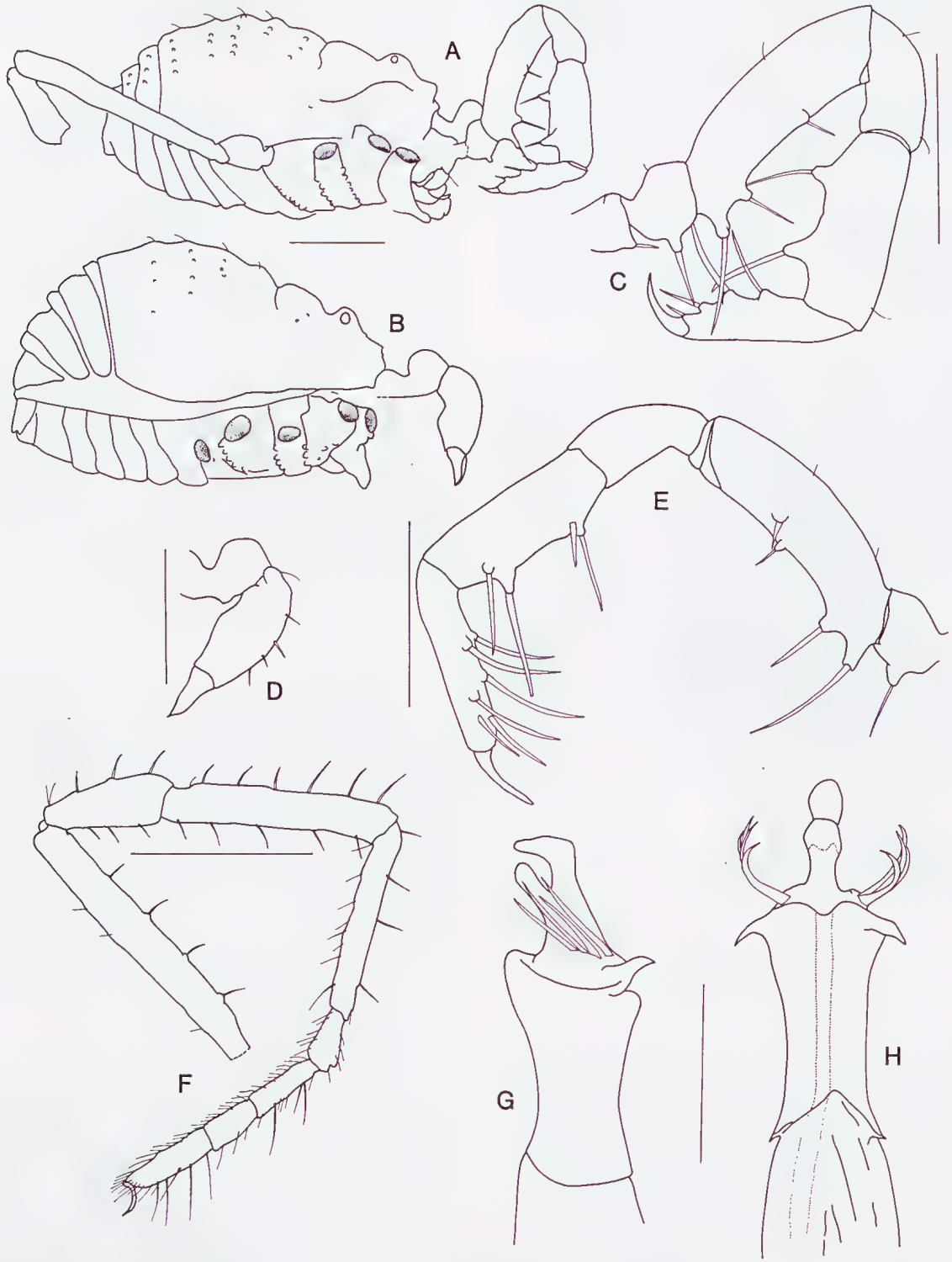

Fig.23. *Lomanella thereseae* n.sp. A,C,D,F-H = male KS23240; B,E = female KS23244. A,B = body and pedipalp, lateral (B distended showing intersclerite membranes); C,E = pedipalp, retro- and prolateral; D = chelicera, lateral; F = right leg I, retrolateral; G,H = penis, lateral and ventral. Scale bars: A-F = 0.5 mm; G,H = 0.1 mm.

approaching the disposition of spines typical of most Australian Triaenonychidae (Fig.1).

Etymology. The specific epithet is in recognition of the extensive biospeleological and surface sampling work of Therese March (formerly Goede) of Fern Tree, Hobart.

Distribution. South-east Tasmania: cave areas, specifically Hastings, Ida Bay and Weld River Arch Caves; surface habitat in Arve Valley near Geevestown.

Lomanella troglodytes n.sp.

Figs 6,7,25

Type material. Southern Tasmania, Precipitous Bluff, 43°30'S 146°35'E: HOLOTYPE male: KS21462, Damper Cave PB-1, A. Clarke, 22 Dec. 1988. PARATYPES: KS21463, Bauhaus Cave, PB-6, S. Eberhard, 24 Dec. 1988, male; KS21465, Cueva Blanca, PB-4, S. Eberhard, 18 Dec. 1988, male; KS23263, Bauhaus Cave, A. Clarke & S. Eberhard, 22 Dec. 1988, male; KS23264, Cave PB-17, A. Clarke & S. Eberhard, 22 Dec. 1988, male.

Diagnosis. Troglobitic, totally blind and depigmented.

Description. MALE. Differs from *L. exigua* in being: cavernicolous, SL 0.96-1.32 (1.10, 5), CW 0.62-0.84 (0.71); body depigmented, overall colour white-straw yellow; blind with no remnant of lens or retina visible, eyemound reduced to slightly raised area which is less prominent than median swelling closer to anterior margin (Fig.6K); body low in profile; process in anteriolateral corners lacking, scute and free tergites sparsely granulate throughout; scutal groove deep, each TA with some small setae arising from tiny granules; pedipalp very long and gracile, PFL 0.57-0.74 (0.66); fv4 very large, trv3 placed at about 0.5 tibia length, its base very prominent; legs extremely attenuated, FIV 1.38-1.66, calcaneus of leg 1 relatively long, femora ventrally without tubercles, claw of tarsus IV much less complex with about 4 lateral branches on each side of the central prong; TF 3(2),5(3),4,4; truncus of penis not swollen distally, sensillar region not elongate proximal to setae; stylus and distal extension to sensillar region more elongate but of similar form; 3 setae visible on each side in lateral view.

FEMALE. Unknown.

Variation. The figures above demonstrate considerable variation in body size and the relative length of appendages. The FIV:CW ratios were 1.64,

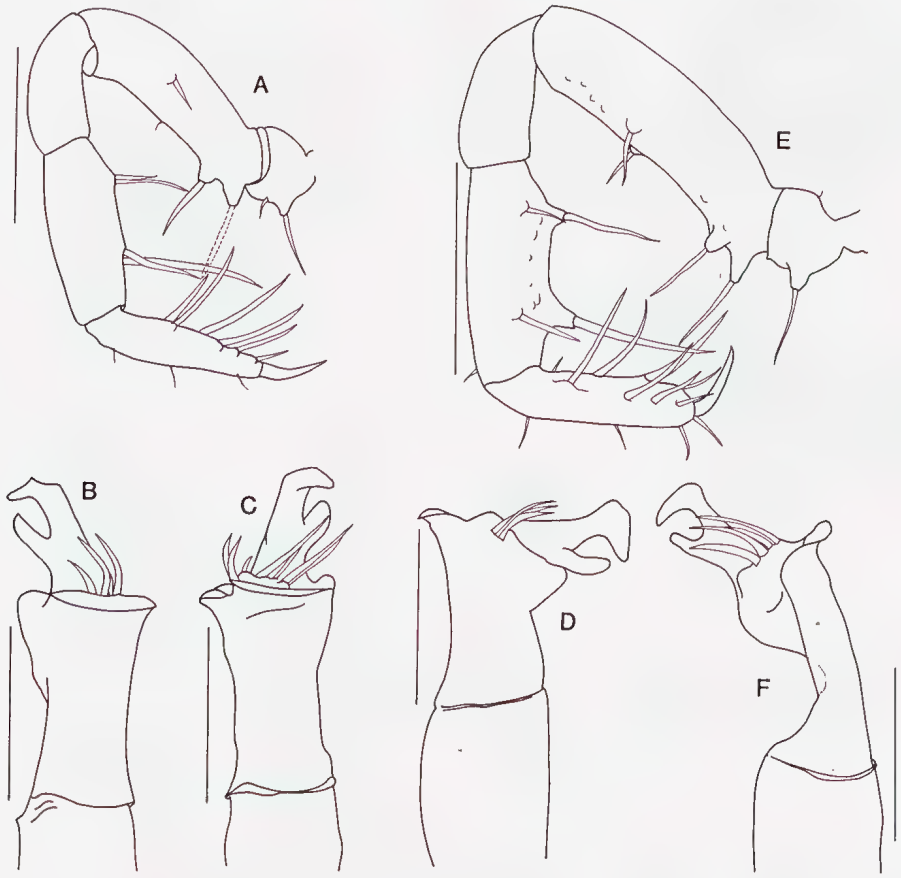

Fig.24. *Lomanella thereseae* n.sp. A-D = *ex* Ida Bay Caves, A = male KS24241; E,F = male KS23260 *ex* Weld River Arch Cave. A,E = pedipalp, prolateral; B,C = penis, lateral and dorsolateral; D = everted penis, expanded (lateral); F = penis, lateral. Scale bars: A,E = 0.5 mm; B,C,D,F = 0.1 mm.

1.97, 2.32, 2.37, 2.44. It is possible these indicate there is polymorphism with regard to 'cave adaptedness' but a larger series is needed to verify this.

Comments. *Lomanella troglodytes* is the most troglomorphic harvestman species in Australia and shows complete eye and pigment loss and great elongation of legs (mean FIV:CW 2.14). It is similar in general habitus to the blind Argentinian triaenonychid *Picunchenops spelaeus* described by Maury (1988). The legs of this latter species are even more attenuated (FIV:CW 3.5) though its eyemound is less reduced in height. *Lomanella troglodytes* appears most closely related to the surface species *L. parva* and *L. quasiparva*. The claw of tarsus IV resembles that of *L. thereseae*.

Of the four species of harvestmen collected in the caves at Precipitous Bluff, three are the most troglomorphic of their respective genera, namely *Hickmanoxyomma cristatum* Hunt, *Lomanella troglodytes* n.sp. and a new species of *Mestonia*. The caves provide a home for several other troglobites (Eberhard, personal communication). Hume (1990) provides access to the speleological literature and cave descriptions.

Etymology. The specific epithet refers to its cave dwelling ecology.

Distribution. Caves at Precipitous Bluff, southern Tasmania.

Lomanella blacki n.sp.

Figs 7,26

Type material. Victoria: HOLOTYPE female: Toolangi State Forest, 4 km south-east of Toolangi, 37°35'S 145°40'E, sieved litter, eucalypt forest, D. Black, 4 Mar. 1990. PARATYPE female: 7 km south on Archeron Way, 15 km east-north-east of Healesville, 37°34'S 145°40'E, sieved tree fern litter, D. Black, 4 Mar. 1990.

Diagnosis. SL less than 1.30 mm, eyemound with short apical tubercle, anteriolateral corners with small tubercles, TF 3(2),4(3),4,4, claw IV with 2 pairs of lateral branches adpressed to median prong.

Description. FEMALE. Similar to *L. exigua* except: body smaller, SL 1.14-1.20 (2), CW 0.65-0.68; dorsum

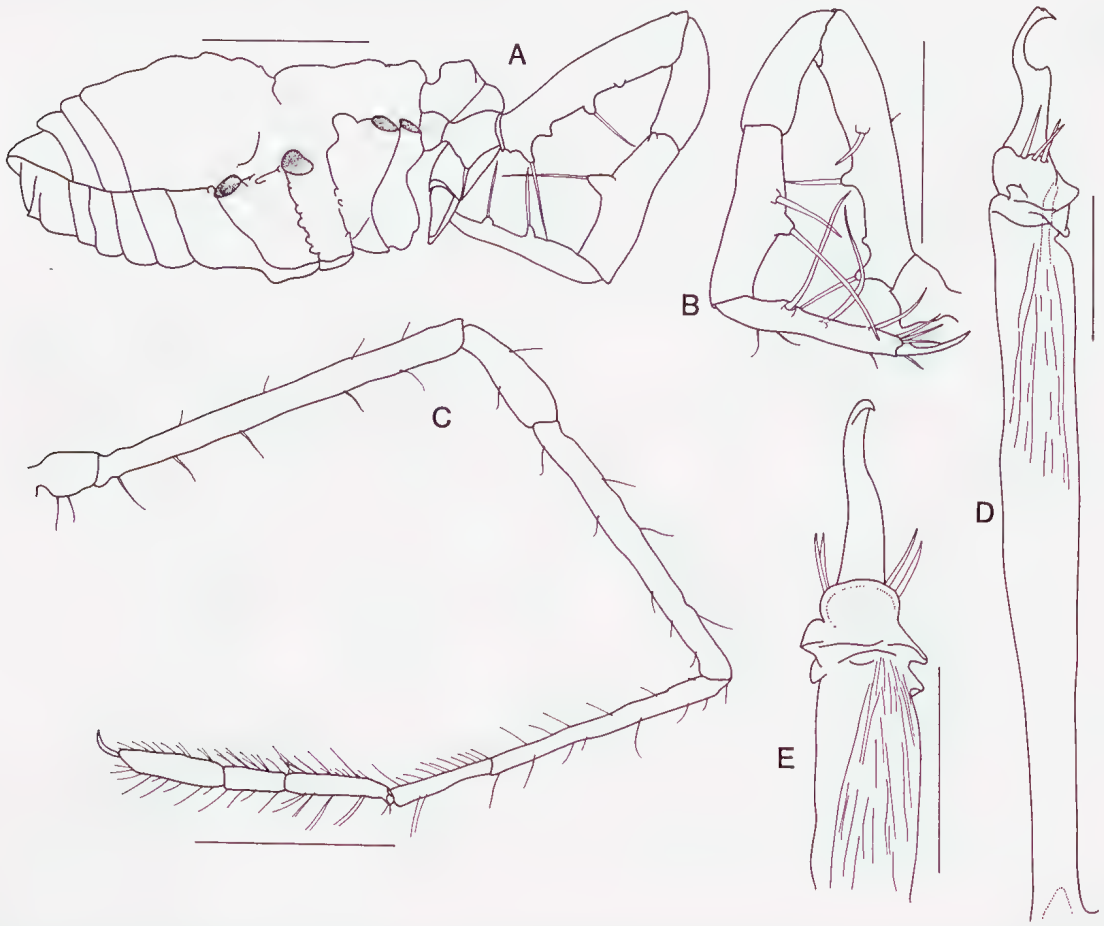

Fig.25. *Lomanella troglodytes* n.sp. A-E = male. A = body and pedipalp, lateral; B = pedipalp, prolateral; C = right leg I, retrolateral; D,E = penis, entire (lateral) and ventral. Scale bars: A-C = 0.5 mm; D,E = 0.1 mm.

predominantly brown interrupted by yellow patches, pigmentation pattern as figured; eyemound rising steeply about 0.8 IOD behind anterior margin, terminating in a small spine and then rounded posterior to eyes; scutal groove deep, extending almost to lateral margins; TA1-5 delineated by prominent grooves; PFL 0.35-0.37, setose tubercles of pedipalp much stronger, tov1, fv1, fv4 and trv3 particularly strong, seta of tarv2 relatively much larger than tarv1; FIV 0.63-0.65, femur I essentially lacking tubercle development; 2 pairs of lateral prongs on claw IV, larger pair about 0.8 length of median prong, adpressed to and lying in concavity along median prong; smaller pair 0.5 length of larger pair, adpressed to and lying in concavity along larger pair (Fig.7C); TF 3(2),4(3),4,4.

MALE. Unknown.

Comments. This is among the smallest bodied species in the genus. Its affinities will remain uncertain until the male is studied. The profile of the eyemound is not unlike females of much larger-bodied species in Victoria, for example *L. kallista* belonging to the *L. raniceps* species group. The structure of the claw of tarsus IV, however, suggests it is transitional between the simple claw of the *L. raniceps* group and the complex peltonychium of the *L. exigua* and *L. peltonychium* species groups. In having claws with two pairs of lateral branches the species resembles the *L. insolentia* species group but in having branches adpressed to the central prong, the species resembles the *L. exigua* and *L. peltonychium* species groups. We predict that the form of the penis will resemble the *L. exigua* group because of pedipalp tibial spination, less than 5 articles in tarsus II and geographical proximity. Discovery of the male of *L. blacki* should greatly assist in understanding the phylogeny of the genus.

Etymology. The specific epithet acknowledges the help of myriapodologist Dennis Black, La Trobe University, Melbourne, collector of the two known specimens of this species.

Distribution. Victoria: Dandenong Range area.

Lomanella peltonychium species group

Western Australia; claw of tarsi II and IV a peltonychium; tarsus II with 5 articles, in lateral view sensillar region of penis reflexed and not extending distal to setae.

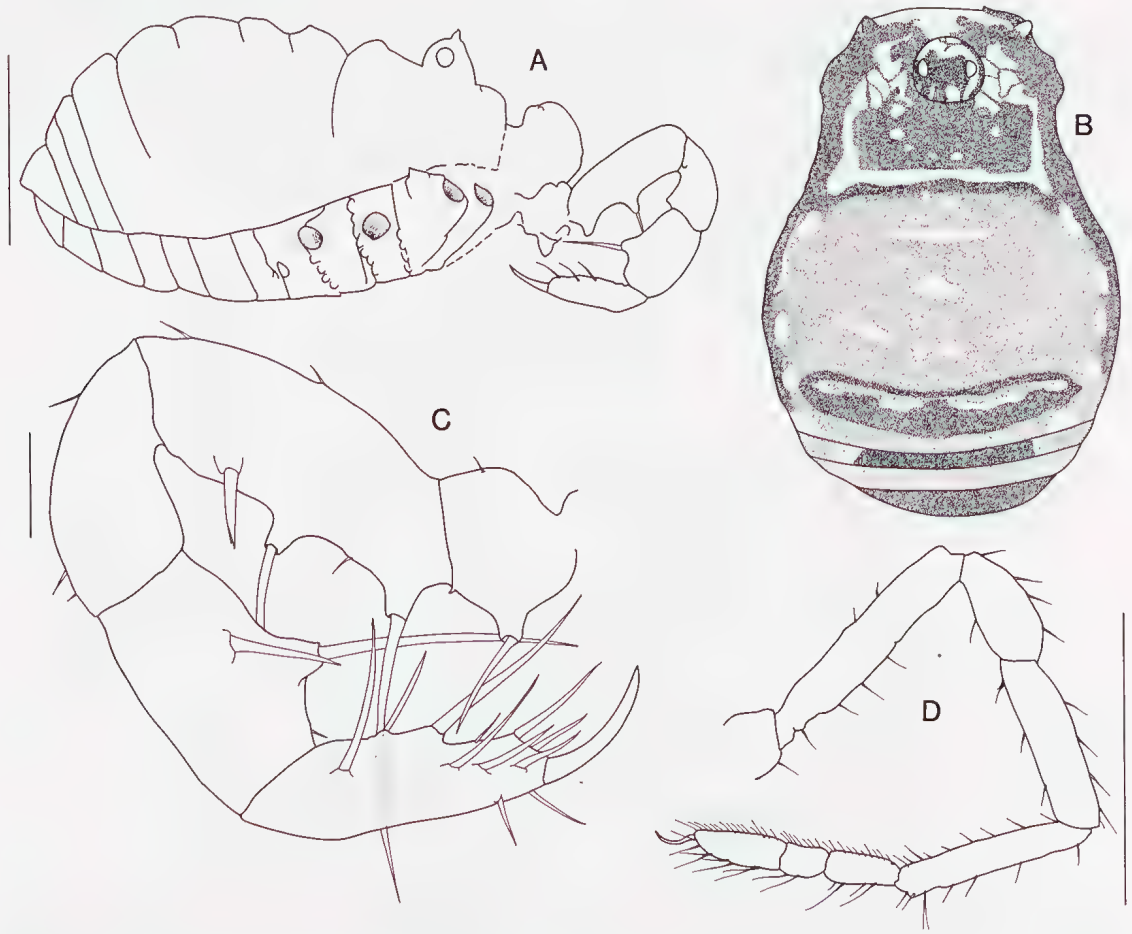

Fig.26. *Lomanella blacki* n.sp. A-D = female; A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C = pedipalp, prolateral; D = right leg I, retrolateral. Scale bars: A,B,D = 0.5 mm; C = 0.1 mm.

Lomanella peltonychium n.sp.

Figs 3,6,7,27

Type material. Western Australia: HOLOTYPE male: ANIC, Nornalup National Park, Walpole, 34°59'S 116°45'E, I.D. Neumann & J.C. Cardale, ANIC berlesate no. 744, 6 Oct. 1981. PARATYPES: ANIC, same data, 20 males, 24 females; KS23270, 11 km north of Walpole, about 180 m, Karri forest, ANIC berlesate no.146, leafmould, R.W. Taylor, 23 Oct. 1969, 5 males, 4 females; ANIC, same data, 2 males, 1 female; WAM 91/1359-62, same data, ANIC berlesate 145, male, 3 females; WAM 90/1703, Walpole Nornalup National Park, Hilltop Road, 4 km south-east of Walpole, J.M. Waldock, 13 June 1987, female.

Other material examined. Western Australia: ANIC, 11 km north of Walpole, about 180 m, Karri forest, ANIC berlesate no.146, leafmould, R.W. Taylor, 23 Oct. 1969, 5

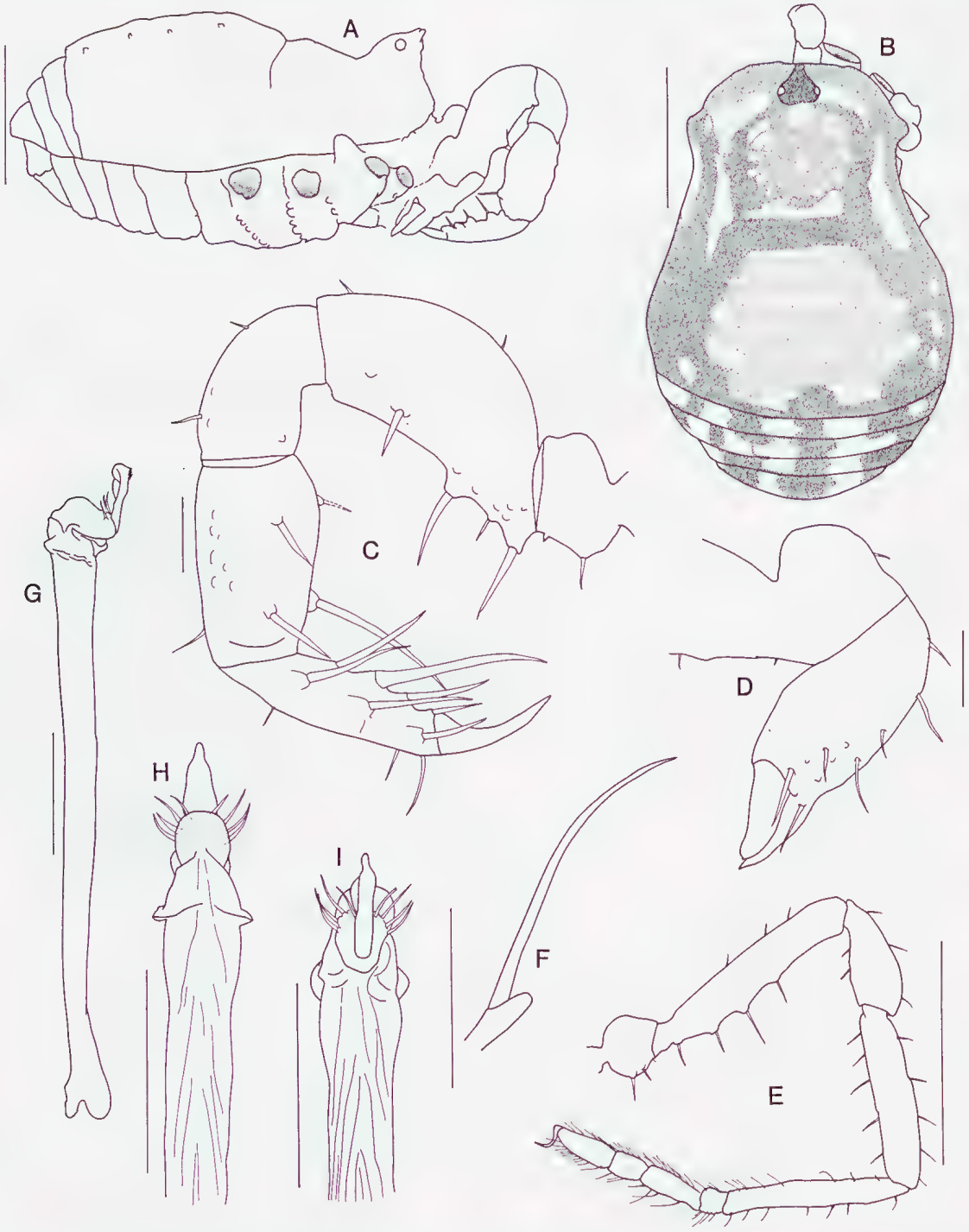

Fig.27. *Lomanella peltonychium* n.sp. A-E = male. A = body and pedipalp, lateral; B = dorsum with pigmentation pattern; C = pedipalp, prolateral; D = chelicera, lateral; E = right leg I, retrolateral; G-I = penis, entire (lateral), ventral and dorsal; F = ovipositor seta. Scale bars: A,B,E = 0.5 mm; C,D,F-I = 0.1 mm.

males, 7 females; ANIC, 19 km north of Walpole, about 250 m, Marri forest, ANIC berlesate no.148, leafmould, R.W. Taylor, 24 Oct. 1969, female; ANIC, 6 km west of Walpole, about 70 m, Karri forest, ANIC berlesate no.142, leafmould, R.W. Taylor, 22 Oct. 1969, 2 males.

Diagnosis. Eyemound conical, rising vertically from short distance behind anterior margin, anteriolateral corners without tubercles or projections, scutal groove extending to near lateral margins, TA1-5 weakly defined by grooves, claws III and IV a peltonychium, 5 articles in tarsus II, penis in lateral view strongly reflexed.

Description. MALE. *Body:* small, SL 1.26-1.33 (1.28, 5); CW 0.75-0.78 (0.76). Pigmentation pattern as figured, dorsum dark brown relieved by yellow-orange patches tending to reflect segmentation in tergal areas. Eyemound rising vertically about 0.5 IOD behind anterior margin, apex anterior to eyes, conical or with small tubercle, eyemound sloping more gradually posterior to apex (Fig.6E); anterior margin of carapace essentially smooth; scutal groove distinct and extending almost to lateral margins (Fig. 6E), TA1-5 not strongly delineated by grooves, groove between TA4 and 5 strongest, each TA and free tergite carrying a row of tiny setose granules, dorsum otherwise uniformly granulate; genital operculum triangular. *Pedipalps:* PFL 0.36-0.42 (0.38); yellowish with brown reticulations; fv1, fv4 and fpl1 moderately developed, fv2 small, fv4 in proximal half; tpv1, tpv2, and strong trv3 present, suggestion of trv2 in some specimens; trv3 much larger than fv1, tarv2 much stronger than tarv1, tarsus with 3 proventral and 4 retroventral setose tubercles. *Legs:* FIV 0.66-0.73 (0.70); ventral surface of femur I with setose tubercles; claws III and IV in form of a peltonychium (Fig.7G inset) with numerous scale-like accessory branches; TF 3(2),5(3),4,4. *Penis:* truncus extremely long; dorsolateral plate in form of a flap-like annulus extending around most of truncus except midventrally; sensillar region in lateral view reflexed with proximal convexity followed by insertion of 4 setae on each side; no extension of sensillar region distal to setae or expression of separate ventral plate; stylus clearly differentiated from sensillar region, distodorsally with a comb of teeth-like processes (Fig.3).

FEMALE. Similar to male, body slightly larger, pedipalps slightly more slender, genital operculum wider at base. Ovipositor with long, unevenly bifid setae (Fig.27F) around vaginal opening (7 on each side in specimen examined). Key measurements: SL 1.33, CW 0.78, PFL 0.38, FIV 0.70.

Comments. The peltonychial claw structure suggests this species is closely allied to the *L. exigua* species group but differs in structure of the penis including the lack of an extension of the sensillar region distal to the setae.

Etymology. The specific epithet is a noun in apposition referring to tarsal claws III and IV which are in the form of a peltonychium.

Distribution. South-west Western Australia.

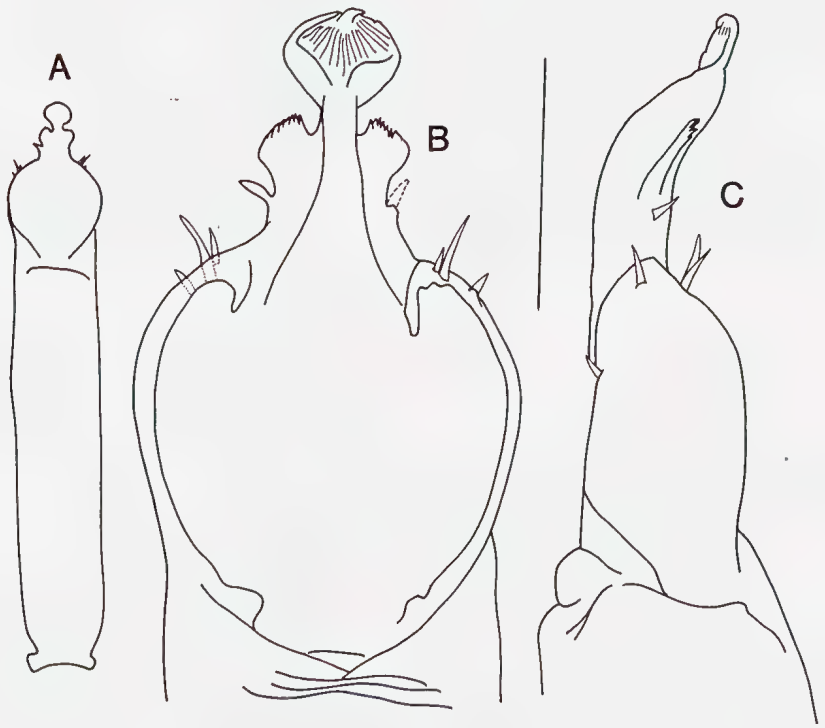

Fig.28. *Nucina silvestris* V.V. Hickman. Holotype. A-C = penis, entire (ventral), ventral and lateral. Scale bar: 0.1 mm.

Nucina silvestris V.V. Hickman

Fig.28

Nucina silvestris V.V. Hickman, 1958: 55-57.

Comments. V.V. Hickman (1958) illustrated the ventral aspect of the penis of this species and stated "The ventral plate is large, oval and concave. The margin is strongly chitinised. Unlike the ventral plate of most other species, it appears to be closely fused with the glans [i.e stylus] and not capable of separate movement. It is provided with three pairs of small inferior setae".

The form of the penis of *Nucina* is clearly convergent with that in certain *Lomanella* spp., particularly *L. raniceps*. The two genera are only distantly related, *Nucina* sharing none of the distinctive synapomorphies of *Lomanella*.

We illustrate the ventral and lateral views and add the following to Hickman's description: small superior seta on each dorsolateral flank of sensillar region, stylus ventrolaterally with a small non-socketed spine and more distally with flat, serrated wing-like process; dorsolateral and dorsal plates lacking.

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APPENDIX

Table 1. Present distribution among taxa of characters used to support family level classifications in the superfamily Travunioidea (Sources: Briggs, 1969, 1971a,b, 1974; Forster, 1954; Hunt, 1990; Martens, 1986; Maury, 1988; Suzuki, 1975a,b, 1976; this paper). X = presence in at least some members of the taxon. 1. Travuniidae; 2. Cladonychiidae; 3. Synthetonychidae; 4. Pentanychidae; 5. Triaenonychidae; 6. Triaenonychinae; 7. Soerensenellinae; 8. Paranonychinae; 9. Kaolinonychinae; 10. Nippononychinae; 11. *Picunchenops spelaeus*; 12. *Lomanella raniceps*; 13. *L. insolentia*; 14. *L. exigua*; 15. *L. peltonychium*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Adult claws III & IV with 1 pair short lateral branches					X	X						X			
1 pair of laterals longer than centralprong					X		X								
2 pairs of laterals				X	X			X					X		
Laterals absent					X	X									
Claw single, then bifurcating		X													
Claw a peltonychium	X		X		X				X	X	X			X	X
Juvenile claw with 3 pairs of laterals	X	X		X	X	X	?	X				X	?		
Juvenile with 4 pairs of laterals					X				X					?	
Juvenile with 5 pairs of laterals					X					X					
Juvenile with no. of laterals dependent on nymphal instar					X										X
Juvenile claw with aroleum		X		X											
Eggs guarded by female							X								
Penis with muscle along length of truncus			X	X	X	X	X	X	X	X	X	X	X	X	X
Muscle at base of truncus	X	X													
Free ninth tergite				X	X*										
Free lateral sclerites	X			X	X	X									

* *Yuria* spp. from Japan, regarded by Suzuki (1975a) as Travuniidae. However, genitalia very similar to *Kainonychus* spp. which Suzuki (1975b) regards as Triaenonychidae. Martens (1986) also regards these as triaenonychids on the basis of penis structure.

ADDENDUM

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Maccullochella ikei, an Endangered Species of Freshwater Cod (Pisces: Percichthyidae) from the Clarence River System, NSW and *M. peelii mariensis*, a New Subspecies from the Mary River System, Qld

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ABSTRACT. The eastern freshwater cod, *Maccullochella ikei*, from the Clarence River system, NSW, is described and *M. peelii mariensis* is described as a new subspecies from the Mary River system, Qld. The Murray cod, *M. p. peelii* and the trout cod, *M. macquariensis*, are indigenous to the Murray-Darling River system. Using electrophoretic data for 19 presumed loci, the coefficient of genetic identity between *M. p. peelii* and *M. ikei* was 0.72 and the banding-patterns of the muscle general protein, liver esterases and five other enzymes, were species-specific. A high proportion of abnormal and inviable hybrid larvae in a cross-breeding experiment indicate that post-zygotic isolating mechanisms have evolved between *M. p. peelii* and *M. ikei*. The coefficient of genetic identity between *M. p. peelii* and *M. p. mariensis* was 0.85 and banding patterns of muscle general protein were diagnostic. Canonical variates analysis using 18 morphological and nine meristic characters, clearly separated both species and the subspecies. *Maccullochella ikei* is distinguished from *M. p. peelii* by having longer pelvic fins, larger orbit length, and larger and morphologically distinct sagittal otoliths. *Maccullochella p. mariensis* differs from *M. p. peelii* by the combination of a deeper and shorter caudal peduncle, longer pelvic fins, larger sagittal otoliths and lesser extension of the first anal pterygiophore towards the first caudal vertebra, and from *M. ikei* by the combination of a deeper caudal peduncle, greater postorbital head length, smaller orbit, larger interorbital width, fewer scale rows below the lateral line, shorter fifth-sixth dorsal spine and lesser extension of the first anal pterygiophore. Although each species has distinctive colouration and mottling, there is some intra-specific variation. *Maccullochella macquariensis* is distinct from the other species by having a straight head profile, jaws of similar length, 14 precaudal vertebrae and distinctive colouration. There was a dramatic reduction in the distribution and abundance of cod in the eastern drainage during the early 1900s and cod were probably extinct in the Richmond and Brisbane River systems by the end of the 1930s. *Maccullochella ikei* and *M. p. mariensis* are each represented by one, small population. Possible causes of the decline, and the management strategies taken to conserve the endangered *M. ikei* are discussed.

ROWLAND, S.J., 1993. *Maccullochella ikei*, an endangered species of freshwater cod (Pisces: Percichthyidae) from the Clarence River system, NSW and *M. peelii mariensis*, a new subspecies from the Mary River system, Qld. Records of the Australian Museum 45(2): 121–145.

The Murray cod *Maccullochella peelii peelii* (Mitchell, 1838) is an Australian native warmwater fish which grows to over 50 kg and is highly regarded because of its size and excellent angling and edible qualities. Murray cod, although no longer common (Rowland, 1989), are found naturally throughout much of the Murray-Darling River system (Fig.1). The trout cod, *M. macquariensis* (Cuvier, 1829) which was once sympatric with *M. p. peelii* in the southern tributaries of the Murray-Darling River system (Berra & Weatherley, 1972), is now found only in the Murray River between Yarrawonga Weir and Tocumwal, and in the upper reaches of Seven Creeks (Ingram *et al.*, 1990) and has been classified as endangered (Harris, 1987).

Murray cod have been introduced into numerous waters outside their natural range including the Cox's, Mulwaree, Nepean and Wollondilly Rivers, Cataract Dam, and several other Sydney water supply dams in the eastern drainage of central NSW (Rowland, 1989). Freshwater cod have also been recorded from the Clarence, Richmond, Brisbane and Mary River systems in the eastern drainage of northern NSW and southern Queensland, but there has always been doubt as to the taxonomic status and origin of the cod in these coastal rivers (Ogilby, 1893, 1895; Anderson, 1916; Lake, 1971). Wilcox (1863) stated that Mr J. Macleay identified a 'Murray River cod' from the Urara

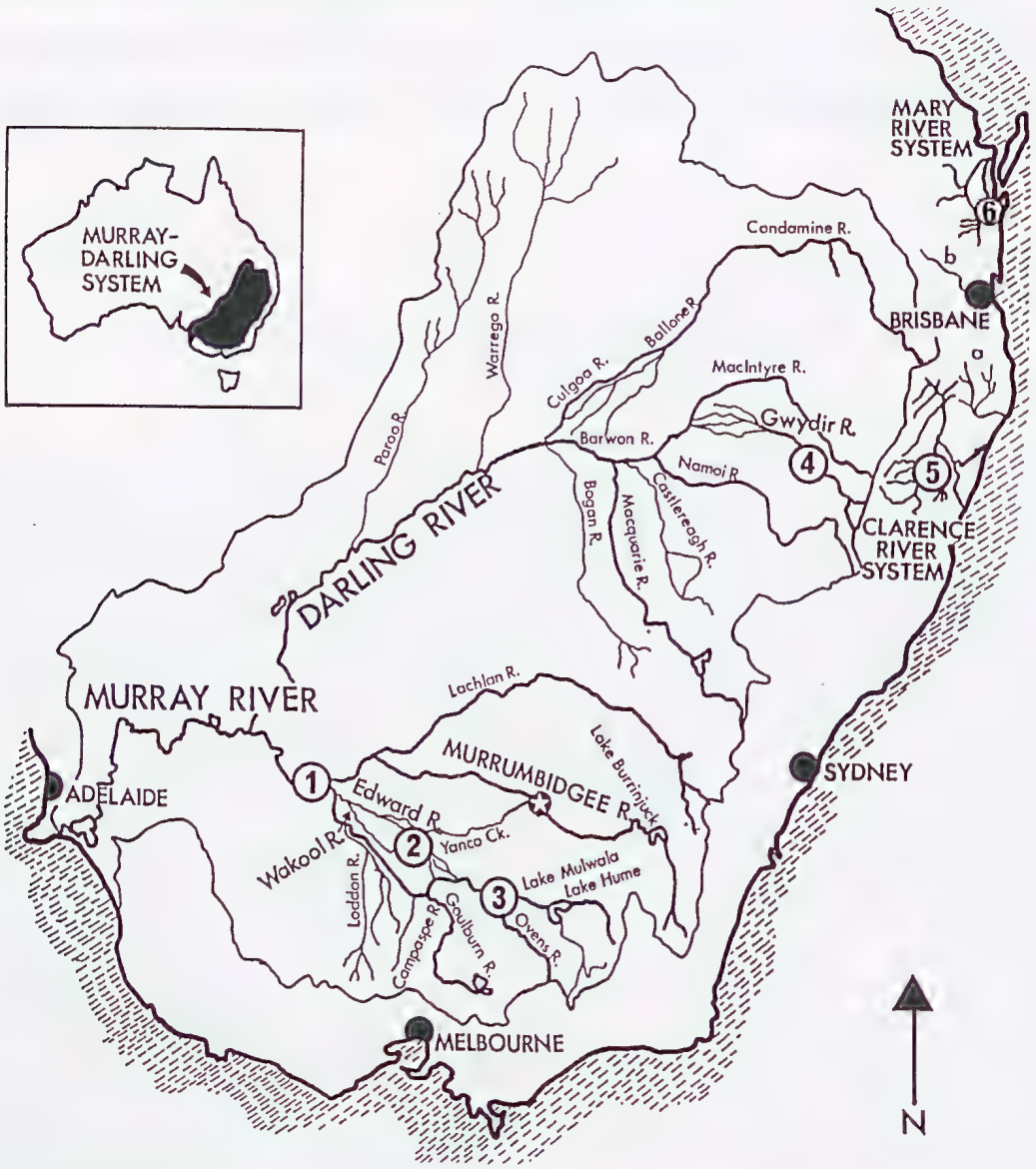

Fig.1. The Murray-Darling, Clarence and Mary River systems: (a) Richmond River system, (b) Brisbane River system. Sampling sites: 1. Murray River; 2. Edward and Wakool Rivers; 3. Lake Mulwala; 4. Gwydir and MacIntyre Rivers; 5. Mann and Nymboida Rivers; 6. Six-mile, Coondoo and Tinana Creeks. Star in circle – Inland Fisheries Research Station.

[sic] (The Orara River is a tributary of the Clarence River) and Hill (1864) stated that Mr James Devlin, who had lived on both the Murrumbidgee and Clarence Rivers, considered that the codfish of the Urara [sic] were identical to those of the western waters. Macleay (1887) obtained a cod from the Richmond River and after comparing it carefully with specimens of *Oligorus macquariensis* and *O. mitchelli* [synonyms of *M. p. peelii* and *M. macquariensis* respectively (Berra & Weatherley, 1972; MacDonald, 1978)] considered that it resembled the latter.

The naturalists on the *Challenger* expedition recorded *O. macquariensis* from the Mary River (Ogilby, 1895), and O'Connor (1897) stated that the Murray cod, *O. macquariensis*, was known to occur in the upper part of the Brisbane River. McCulloch and Whitley (1925) also recorded *O. macquariensis* from these two rivers as well as the tributaries of the Darling River in Queensland. Two forms of cod – 'sharp-nose' and 'boof-headed' – are currently recognised in the Mary system (Merrick & Schmida, 1984), and experienced anglers have long recognised morphological and biological differences between cod from the Mary River and those from the Murray-Darling system in southern Queensland (J. Winkel, personal communication).

Whitley (1937) and Berra & Weatherley (1972) included museum specimens of cod from the Mary River in their systematic reviews of *Maccullochella*, but details of the number and size of these specimens were not given. MacDonald (1978) did not include cod from the eastern drainage in his review of the systematics of Australian freshwater percichthyid fishes. The cod population in the Clarence River system was recognised as a distinct species by Rowland (1985) and a description of *Maccullochella ikei* n.sp., without details of the type material, was published by Rowland (1986). In the current paper, the research to determine the taxonomic status of the cod populations in the eastern drainage is detailed. Data on the type material of *M. ikei* are presented, and *M. peelii mariensis* is described as a new subspecies from the Mary River system. Historical records were examined, and residents of north-eastern NSW and south-eastern Queensland were interviewed to enable a qualitative comparison of the past and present distribution and abundance of cod in the eastern drainage.

Materials and Methods

General. Cod were sampled from the Murray-Darling, Clarence and Mary systems (Fig.1). In addition, Murray cod that had been artificially bred at the Inland Fisheries Research Station (IFRS) and stocked into farm dams near Narrandera, were sampled when one to three years old. The number and range in standard length (SL) of cod sampled from each site are given in Table 1 [Appendix]. After capture, morphometric data were recorded and liver tissue and muscle tissue from midway between the base of the pelvic fin and the anus, were removed from some specimens, frozen and kept at -20°C until required for electrophoresis. Additional specimens of cod from the Clarence system were examined live in the field, under anaesthetic, and released.

All measurements and counts were made on fresh specimens with the exception of those for the type specimens which were made within two months of fixation in 10% formalin and preservation in 70% alcohol. In the descriptions, proportions and counts for the lectotype of *M. ikei* and the holotype of *M. p. mariensis* are followed, in parentheses, by the range of each character for the paralectotypes, paratypes, other material and other specimens. AMS and QM are prefixes for specimens lodged at the Australian Museum, Sydney and Queensland Museum, Brisbane respectively.

All tables are listed in the Appendix.

Electrophoresis. Electrophoresis was carried out on slab polyacrylamide gels, horizontal starch gels and cellulose acetate sheets using techniques described by Shaw & Prasad (1970), Keenan & Shaklee (1985) and Shaklee & Keenan (1986). Details of the six electrophoretic systems used are given in Table 2 and the proteins that were assayed, the systems and tissues used and the number of cod analysed are given in Table 3. Tissues for starch gel and cellulose acetate electrophoresis were homogenised in a lysing solution (100 mL H_2O, 2 drops MCE, 100 uL NaDP) and centrifuged at 5000 rpm for 5 min at 4°C. Presumptive gene loci are labelled with an italicised abbreviation for the enzyme (Table 3) and multiple loci for a given enzyme are distinguished by numerals, with 1 representing the most anodally migrating isozyme. Allozymes of common mobility are interpreted as if encoded by the same allele. Alleles were designated by their relative mobility, with the most anodal being 100.

The genetic identity and genetic distance between cod from the Murray-Darling, Clarence and Mary systems were estimated using the coefficient of genetic identity (I) and genetic distance (D = -ln I) as defined by Nei (1972). Values of I can range from 0 where the populations being compared share no alleles, to 1, where all alleles are common and have the same frequency. Estimates of the divergence times between cod in the different systems were calculated using $t = 5 \times 10^6 D$ (Nei, 1975) where t = time since divergence in years, and D = genetic distance.

Morphometrics. Meristics and morphological measurements follow Hubbs & Lagler (1974) except where stated. The respective measurements were made on the left side of the fish where possible using a measuring board (to the nearest 1 mm) and vernier callipers (to nearest 0.1 mm). The post-orbital and orbit lengths, the inter-orbital width and the width between the posterior nares were least-fleshy measurements. Body depth I is the distance between the base of the first dorsal spine and the base of the pelvic fin and body depth II is the maximum depth when the fish is held

vertically by the lower jaw. The length of the pelvic fin was measured from the base of the fin to the tip of the longest filament when extended.

Data on the 27 characters listed in Tables 6 and 7, plus the number of spines in the anal fin, the number of rays in the pelvic fin and the number of pyloric caecae were recorded. Head characters were expressed as a percentage of head length (HL) and all other measurements, including HL, were expressed as a percentage of SL for each specimen. These data were subjected to a canonical variates analysis (CVA; Reyment *et al.*, 1984). Only cod with values for all characters listed in Tables 6 and 7 except body depth I were included in the analysis. The first and second canonical variates were plotted to identify the distinct forms of cod, and the canonical structures were listed to identify the main characters contributing to the variation. The means of each morphometric character for cod from the Clarence system, the Mary system and Murray cod from rivers and farm dams were then compared using Student's t-tests; this analysis was also used to compare the means of the characters for Murray cod from rivers and farm dams and from Lake Mulwala. To reduce the effect of allometric growth of the various body parts on the analysis, only Murray cod (with the exception of those sampled from Lake Mulwala) that were within the length range of cod sampled from the Clarence and Mary systems were analysed. Berra & Weatherley (1972) found that eye diameter and the length of the longest dorsal spine grew allometrically in Murray cod, and so the means of all characters except orbit length and the length of the fifth or sixth dorsal spine were compared between populations of Murray cod.

Osteology. X-rays were made of preserved specimens of Murray cod (n=3), trout cod (3), and cod from the Clarence (4) and Mary (5) systems. The predorsal bones, and the precaudal and caudal vertebrae were counted in each specimen. In this study, vertebrae anterior to the vertebra associated with the first anal pterygiophore were classified as precaudal vertebrae. The length of the first anal pterygiophore was measured (on the X-rays) and expressed as a percentage of the distance from the base of this pterygiophore to the ventral surface of the first caudal vertebra.

Otoliths. The lengths and widths of otoliths from five Murray cod (total length, TL 420-625 mm), five cod from the Clarence system (TL 330-489 mm) and four cod from the Mary system (TL 420-610 mm) were measured using vernier callipers and expressed as a percentage of the TL for each fish. The otoliths were then lightly smeared with graphite to emphasise external morphological features and compared.

Cross-breeding experiment. Four cod (1 male, 3 females) were captured from the Clarence system and transported live to the IFRS for use in a cross-breeding experiment with Murray cod that had originally been captured from the Murrumbidgee River. All cod were held in earthen ponds until October. Experiments involving cod from the Mary River system and trout cod were not conducted because of the logistical problems with catching, transporting and maintaining the broodfish, the limited facilities at IFRS and the general difficulty of breeding freshwater cod.

Techniques for the handling, injection of human chorionic gonadotrophin (HCG), stripping, and the fertilisation and incubation of eggs are described by Rowland (1988a). The only male cod from the Clarence system died after the injection of HCG and so reciprocal crosses involving this male were not possible. Milt from two Murray cod males were used to fertilise eggs. The eggs from each female were incubated in separate troughs at temperatures ranging from 20 to 24°C. The hatch rate of eggs from each female was determined by expressing the number of larvae that hatched as a percentage of the number of eggs incubated. Larvae from each batch of eggs were sampled daily and examined microscopically, and differences between Murray cod and hybrid larvae were noted.

Results

Electrophoresis – general proteins. The phenotypes of general protein following polyacrylamide gel electrophoresis of cod muscle tissue are shown in Figure 2. The banding patterns at three zones (1, 2, 3) were diagnostic for cod from each of the three systems; cod from the Clarence and Mary systems differed at zone 1, cod from the Clarence and Murray cod at zones 2 and 3, and cod from the Mary system differed from Murray cod at all three zones. The banding patterns of Murray cod from all sampling sites (including Lake Mulwala; No. 24) were indistinguishable, with the exception of fish No. 1 which had a distinct band anodal to the diagnostic fast band at zone 3 (Fig.2). This cod was from the Gwydir River in northern NSW Fish No. 4 was also from this river and its banding pattern was identical to that of all other specimens of Murray cod.

Enzymatic proteins. The ten loci encoding the first eight enzymes listed in Table 3 were monomorphic and fixed for the same allele in all cod. The most anodal isozyme of aspartate amino-transferase (*Aat-1*) consisted of two bands and the isozymes of the other non-diagnostic enzymes consisted of single, generally intensely-staining bands. The malate dehydrogenase isozyme consisted of two bands, with the most anodal band having greater intensity in tissue from Murray cod and cod from the Mary system, whereas the cathodal band stained more intensely in tissue of cod from the Clarence system. Allelic frequencies at loci of diagnostic enzymes after starch gel and cellulose acetate electrophoresis of cod muscle and liver tissue are given in Table 4.

Mannose-6-phosphate isomerase (MPI). The enzyme MPI varies genetically in a wide variety of organisms but generally behaves as a monomer exhibiting single-banded homozygotes (Shaklee, 1983). All cod examined had a single, intensely-staining band at one locus, *Mpi-1*. Murray cod and cod from the Clarence system were fixed for alternative alleles (100, 87) at this locus, and cod from the Mary system were fixed for the allele characteristic of Murray cod.

Isocitrate dehydrogenase (IDH). The $NADP^+$-dependent IDH of teleost fishes often appears in both supernatant and mitochondrial forms (Engel *et al.*, 1971; Wheat *et al.*, 1973). Two isozymes of IDH were observed after electrophoresis of cod muscle tissue and the lack of interlocus heterodimers suggests that the observed phenotypes represent one supernatant and one mitochondrial loci. All cod were fixed for the same allele at *Idh-1*, but Murray cod and cod from the Clarence system were fixed for alternative alleles at *Idh-2*. The phenotypes at this locus of cod from the Mary system were not determined.

L-iditol dehydrogenase (IDDH). Two loci control the expression of IDDH phenotypes in cod liver tissue. At *Iddh-1*, Murray cod and cod from the Clarence system were fixed for alternative alleles (100, 88). Five cod from the Mary system displayed the allele characteristic of Clarence fish but one cod (captured from Tinana Creek) displayed the allele characteristic of Murray cod. No heterozygous forms were observed and the cod from Tinana Creek was otherwise electrophoretically identical to the other cod from the Mary system.

Glucose-6-phosphate isomerase (GPI). GPI in fishes is a dimeric molecule and multiple isozymes result from the interaction of subunits (Avise & Kitto, 1973). Two types of subunits predominate in nearly all tissues (Shaklee *et al.*, 1974). The GPI phenotypes observed after electrophoresis of cod muscle tissue were presumed to represent the homodimers *Gpi-*A_2 and *Gpi-*B_2 and the *AB* heterodimer. *Gpi-*B_2 did not stain intensely although slight variation was evident, different phenotypes were not allocated to individual fish. *Gpi-*A_2 stained intensely. Murray cod and cod from the Mary system were fixed for the 'fast' band and cod from the Clarence were fixed for the 'slow' band.

Glycerol-3-phosphate dehydrogenase (G3PDH). Broad bands of G3PDH activity were apparent after starch gel electrophoresis of cod muscle tissue. There were two relative mobilities of the bands – 'fast' and 'slow' – and it was assumed that these represented alleles at a single G3PDH locus. Again, Murray cod and cod from the Clarence system were fixed for alternative alleles (100, 90) and the cod from the Mary system all had the allele characteristic of Murray cod.

Glucose-6-phosphate dehydrogenase (G6PDH). Multiple allozymes were resolved by electrophoresis of cod liver tissue, but positive interpretation was not possible because the molecular and genetic bases of teleost G6PDH are poorly understood (Shaklee *et al.*, 1974). It is tentatively proposed that two loci control the expression of G6PDH phenotypes in cod liver tissue and that there are five alleles at the *G6pdh-1* locus. Other possible interpretations of the observed phenotypes are

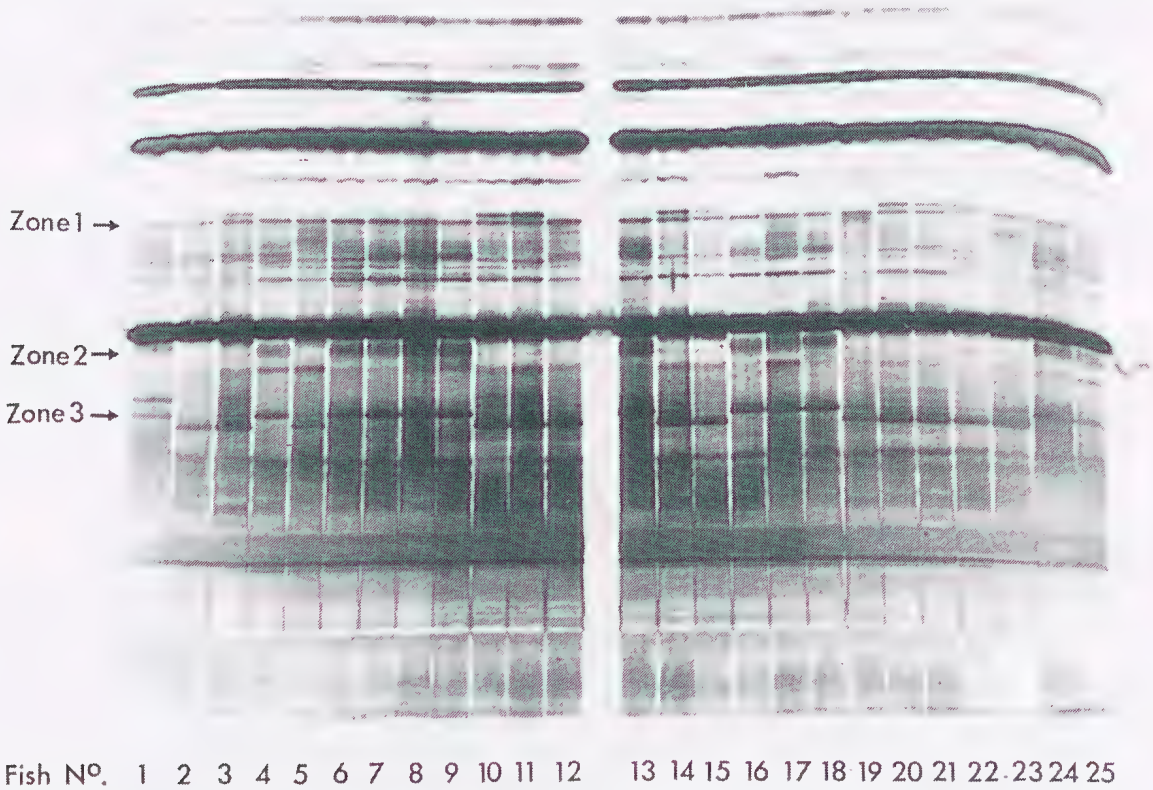

Fig.2. General protein phenotypes of cod after polyacrylamide gel electrophoresis of muscle tissue. *Maccullochella p. peelii*: fish nos 1, 4, 6, 7, 8, 9, 13, 16, 17, 18, 24, 25; *Maccullochella ikei*: fish nos 2, 5, 12, 19, 23; *Maccullochella p. mariensis*: fish nos 3, 10, 11, 14, 15, 20, 21, 22.

multiple loci, heterodimers and post-translation changes. There was a significant difference (X^2=183.56, df=8, P less than 0.005) in the frequency of the presumed alleles at *G6pdh-1* between Murray cod and cod from the Clarence and Mary systems. The two alleles (92, 69) with the highest frequency in Murray cod, were either absent or present at low frequencies in cod from the eastern drainage (Table 4). Although there appeared to be some variation at *G6pdh-2*, resolution of this locus was relatively poor and so different phenotypes were not allocated to individual fish.

Esterases (EST). There were three major zones of activity in cod liver tissue and at zone 2, bands of different mobility characterised Murray cod and cod from the Clarence system. EST phenotypes of cod from the Mary system were not determined because of poor resolution.

Genetic identity, genetic distance and time since divergence. Electrophoretic data from 19 loci were used to calculate the coefficients of genetic identity. The data for general protein, esterases, malate dehydrogenase ($NADP^+$) and *G6pdh-2* were not used because the genetic basis of the former two proteins is not known and the interpretation of phenotypes at *Mdh ($NADP^+$)-1* and *G6pdh-2* was uncertain.

The coefficients of genetic identity (I) and the genetic distance (D) between Murray cod, cod from the Clarence and Mary systems and trout cod [data from MacDonald (1978)] are given in Table 5.

The electrophoretic data derived from the enzymatic proteins strongly suggest that cod in the Clarence system represent a separate species to *M. p. peelii* (I=0.72, D=0.33) and that the population is not conspecific with cod in the Mary system (I=0.73, D=0.32). The electrophoretic data also suggest that the cod population in the Mary system is more closely related to *M. p. peelii* (I=0.85, D=0.16) than to cod in the Clarence system.

The estimates of the time of divergence of *M. p. peelii* and cod in the Clarence and Mary systems from a

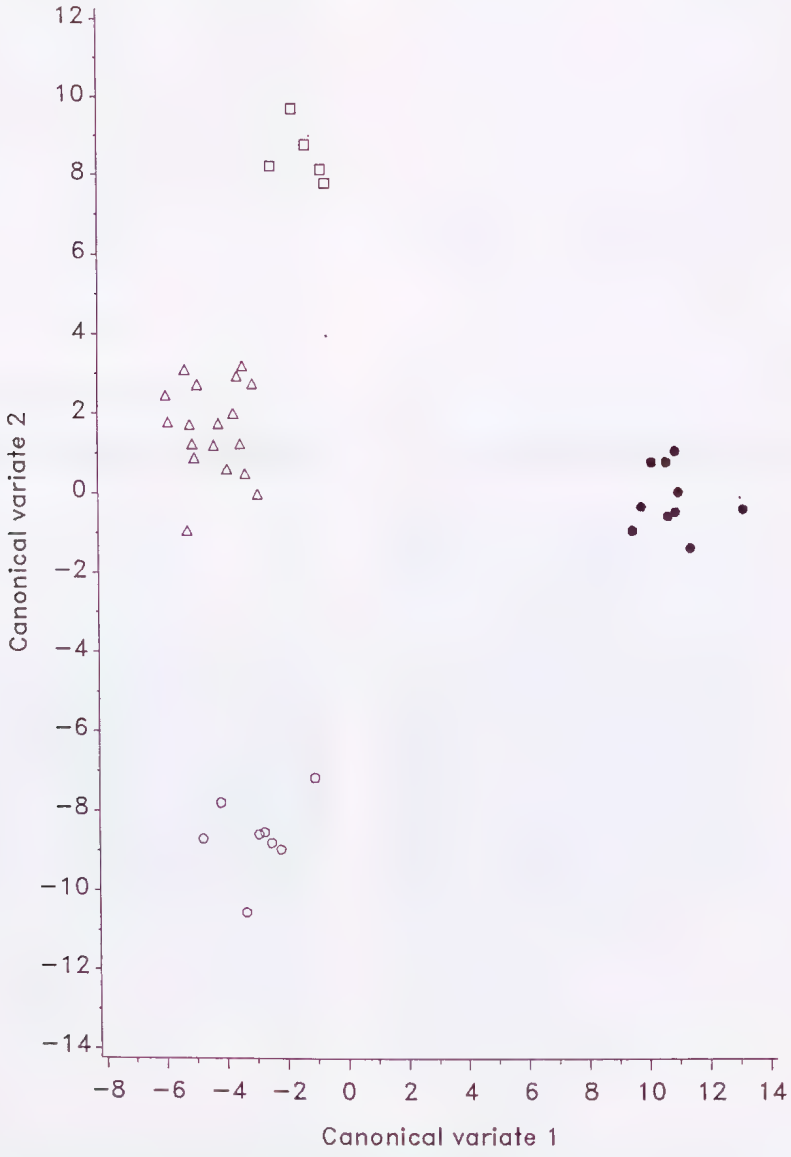

Fig.3. Plot of first and second canonical variates. Dot – *M. ikei*, circle – *M. p. mariensis*, square – *M. p. peelii* ex Lake Mulwala, triangle – *M. p. peelii* ex rivers and farm dams.

common ancestor are 1.7 and 0.8 million years ago (mya) respectively.

Morphometrics – canonical variates analysis. The number of spines in the anal fin (3), rays in the pelvic fin (5) and pyloric caecae (4) were the same in all cod examined and hence not entered into the CVA. The CVA of the remaining 27 characters separated cod into four distinct groups: cod from the Clarence system; cod from the Mary system; Murray cod from rivers and farm dams; Murray cod from Lake Mulwala (Fig.3). Cod from the Clarence system were separated from the other populations by the first canonical variate on the basis of postorbital head length, scale rows below the lateral line, length of the fifth/sixth dorsal spine, length of the pelvic fin and interorbital width. The second canonical variate separated the remaining three populations on the basis of length of pelvic fin, anal base, depth of caudal peduncle, and orbit length.

The means of seven morphometric characters differed significantly (P less than 0.01) between Murray cod from the rivers (and farm dams) and those sampled from Lake Mulwala (Table 6). These data demonstrate substantial intraspecific morphological variation between populations in rivers and small, impounded waters and those in large, impounded waters.

Comparison of Murray cod and cod from the Clarence system. These cod have distinctive colouration. Cod from the Clarence system are generally yellow-green to golden with black to very dark green, heavily reticulated mottling on the dorsal surface, head and sides, whereas in Murray cod the colour ranges from cream to olive to yellow-green with relatively smaller, pale to dark green mottling often with small dark spots between the reticulation (Fig.4). The pelvic fin of Clarence cod is clear, whereas in Murray cod this fin is usually whitish.

The means of 13 morphometric characters differed significantly (P less than 0.01) between Murray cod and cod from the Clarence system (Table 7). The ranges of the length of the pelvic fin (expressed as a percentage of SL) do not overlap, thus providing a diagnostic character. The second filament on the first ray of the pelvic fin is usually extended in cod from the Clarence system compared to Murray cod (Fig.4). The fine tip of this filament may be damaged or missing in preserved specimens. Orbit length is also diagnostic.

Cod from the Mary system. These cod differ significantly (P less than 0.01) in ten characters from Clarence cod and in five characters from Murray cod (Table 7). Although there is no single morphometric character which is completely diagnostic because the ranges of all characters overlap, a combination of characters enables diagnosis. These data and the results of the CVA indicate that cod from the Mary system are morphometrically more similar to Murray cod. However, the means of the length of the pelvic fin (expressed as a percentage of SL) were significantly different (P less than 0.001), and the range of this character in the Mary system population lay mainly within the range of the character for the Clarence population (Table 7). The relatively long pelvic fin is therefore common to the populations of cod in the eastern drainage. Cod in the Mary system also have a dark, heavily reticulated mottled pattern, similar to cod in the Clarence system (Fig.4).

Osteology

Cod from the Clarence system and Murray cod had a total of 35 vertebrae, consisting of 15 precaudal and 20 caudal vertebrae. The three trout cod examined each had 14 precaudal and 21 caudal vertebrae and three of the five cod from the Mary system had 35 (15 + 20) vertebrae, while the other two had only 34 (15 + 19) vertebrae (Table 8). The extension of the first anal pterygiophore towards the first caudal vertebra is greater in Murray cod and cod from the Clarence system than in trout cod and cod from the Mary system.

Otoliths

The sagittal otoliths of *Maccullochella* spp. are relatively large and long (length:width, 2.2-2.8:1), and show some inter-specific differences. Otoliths of cod from the Clarence system (otolith length 3.2-3.5% of fish TL) and the Mary system (2.9-3.3% TL) are larger than otoliths from similar-sized Murray cod (2.5-2.9% TL). In cod from the Clarence system the anterior edge of the rostrum of each otolith is more rounded and has a distinctly smaller antirostrum than otoliths in Murray cod. The medial dorsal surface is slightly indented whereas in Murray cod this surface is slightly convex. The morphology of otoliths in cod from the Mary system appears intermediate to those in Murray cod and cod from the Clarence system.

Cross-breeding Experiment

The results of the hormone-induced breeding trials are presented in Table 9. Dosages of 500 and 1000 IU/kg HCG did not induce ovulation in cod from the Clarence system, however, as expected (Rowland, 1988a) ovulation had commenced in female Murray cod 48 h after the injection of 1000 IU/kg HCG. Two batches of eggs were stripped after different latent periods from each female. The hatch rates of eggs stripped 48 and 48 h after injection were 3 and 58% respectively, and the hatch rates of eggs stripped 49 and 50 h after injection were 90 and 75%. Approximately 96,200 eggs were stripped and a total of 50,125 larvae hatched. All larvae underwent normal development during yolk sac

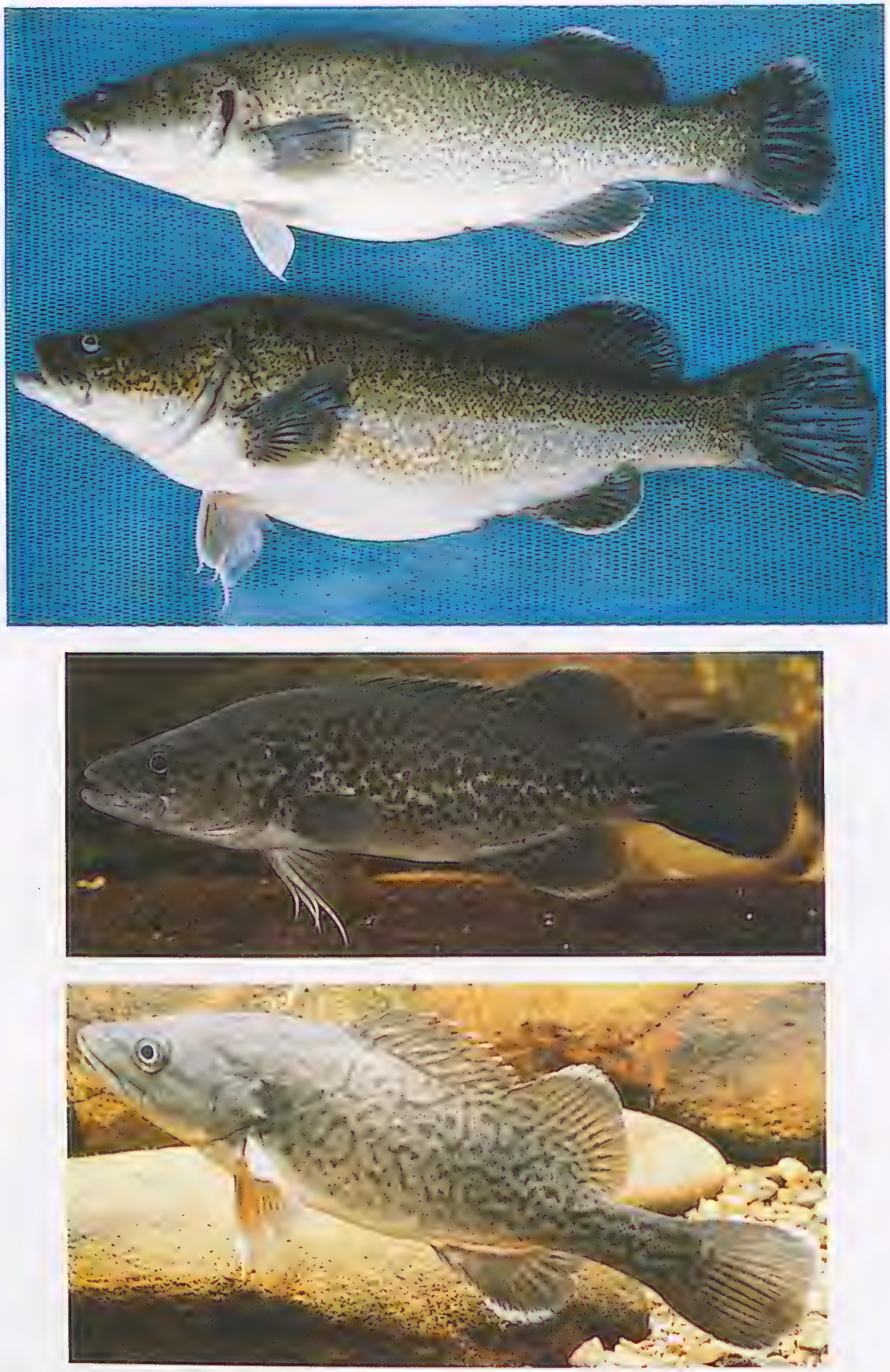

Fig.4. (top) *Maccullochella peelii peelii* (female, 495 mm SL, 554 mm TL, 3.1 kg total weight, left operculum damaged), (upper middle) *Maccullochella ikei* (female, 515 mm SL, 610 mm TL, 3.4 kg total weight) (photographed live, under anaesthetic by Ken Bock), (lower middle) *Maccullochella peelii mariensis* n.subsp. (photograph, Gunther Schmida) (bottom) *Maccullochella macquariensis* (250 mm TL) (photograph, Gunther Schmida).

absorption, confirming that the milt from the two males was viable.

Ovulation had commenced in a female cod from the Clarence system 46 h after the injection of 2000 IU/kg HCG. Approximately 6,750 eggs were stripped and fertilised using milt from the two Murray cod males. An additional 1,900 eggs were stripped and fertilised two hours later. Hatching commenced 120 h after fertilisation. A total of 777 eggs hatched (9% hatch rate), comprising 147 (2%) of those stripped 46 h after injection and 630 (33%) stripped after 48 h (Table 9).

Most hybrid larvae that hatched from both batches of eggs were obviously deformed. The deformities ranged from gross malformations of the head, body and tail (Fig.5a) to scoliosis and/or lordosis (Fig.5b). Other abnormalities observed in most hybrid larvae were: malformation of the fins, in particular the caudal and pectoral fins; the lack of, or decreased size of the oil droplet; a relatively pale pink colour of blood in comparison to the bright red blood of Murray cod larvae. Abnormal larvae of Murray cod are very uncommon even when hatch rates are low due to suboptimal induced-spawning conditions (Rowland, 1988a).

There were also some developmental differences between Murray cod and the small number of apparently 'normal' hybrid larvae. The oil droplet in these hybrid larvae was spherical and positioned below the gills, whereas in Murray cod larvae the oil droplet was oval-shaped and situated below the eyes (Fig.6). The cardiac cavity, when viewed laterally, was distinctly narrower in Murray cod than in hybrid larvae.

At the completion of yolk sac absorption, approximately ten days after the completion of hatching, only 226 hybrid larvae were alive (29% of the total that had hatched). At this stage of development, hybrid larvae averaged 10.7 mm TL (n=12) and were significantly smaller (t=10.3, P less than 0.01) than same-aged Murray cod larvae, that averaged 13 mm TL (n=12). Most hybrid larvae were much less active and died within two weeks of yolk sac absorption.

The abnormalities observed in hybrid larvae, the high mortalities during and after yolk sac absorption and the developmental differences between Murray cod and

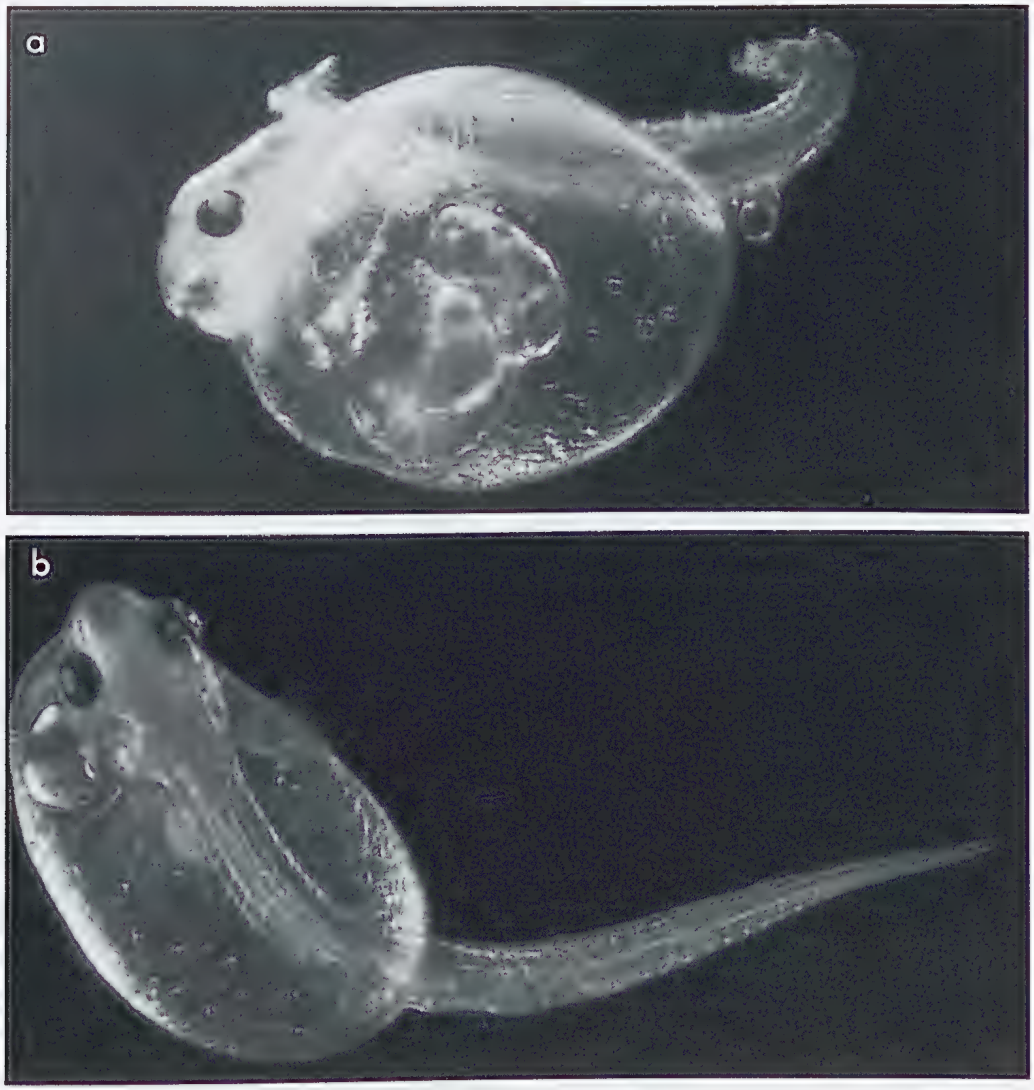

Fig.5. Abnormal larvae (50 h old) from a cross between eastern freshwater cod and Murray cod (x22), (a) grossly abnormal larva, (b) larva with scoliosis (photograph, P.M. Selosse).

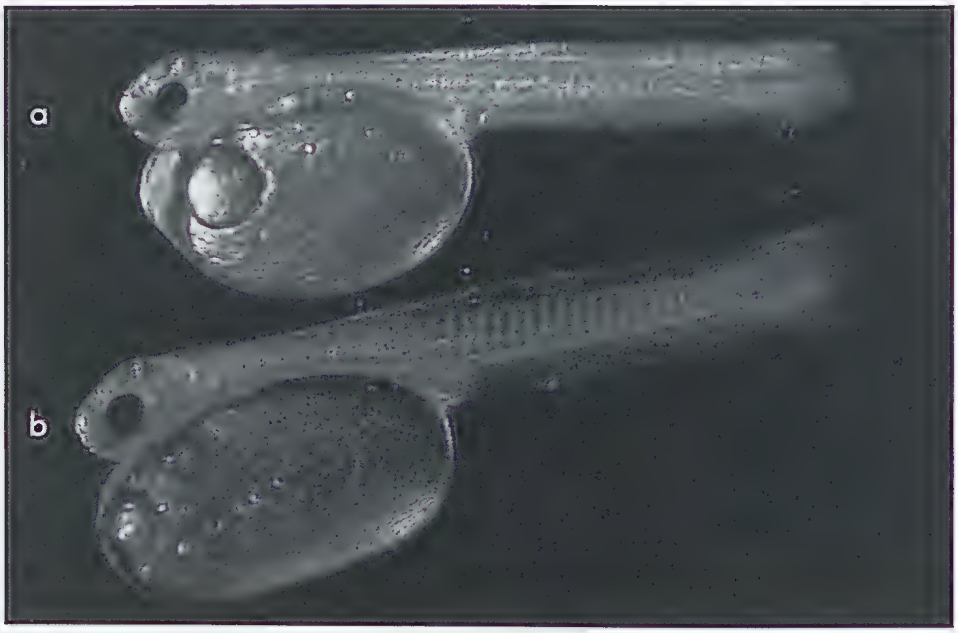

Fig.6. Cod yolk sac larvae 72 h old (x15), (a) from cross between eastern freshwater cod and Murray cod and (b) Murray cod (photograph, P.M. Selosse).

hybrid larvae, suggest that hybrid breakdown was occurring and that post-zygotic isolating mechanisms have evolved between *M. p. peelii* and the cod in the Clarence system.

As a result of the morphological and genetic differences between *M. p. peelii* and cod from the Clarence system, and the inviability of hybrid larvae, the eastern freshwater cod is considered to be a distinct species.

Maccullochella ikei Rowland, 1986

eastern freshwater cod

Fig.7

Gristes peelii.–Bennett, 1864: 81 (in part, in rivers of the eastern ranges).

Macquaria peelii.–Anon., 1859: 5 (large fish from Eurara [sic] River donated to Australian Museum by Mr Wilcox.).–Angas, 1860: 5 (from the Clarence River presented by Mr J.F. Wilcox).

Oligorus macquariensis.–Macleay *et al.*, 1880: 36 (in part, in branches of the Clarence).–Tenison-Woods, 1883: 103 (in part, in a few of the eastern rivers to the north of Sydney).–Ogilby, 1886: 13 (in part, northern rivers of the eastern watershed of NSW).–Ogilby, 1893: 19 (in part, found in some of the northern coastal rivers of the Colony).–Thompson, 1893: 21 (in part, in Clarence system).–Ogilby, 1895: 71, 72 (in part, native of the Richmond and Clarence Rivers district).–McCulloch, 1922: 46, 57 (in part, in the headwaters of some northern streams).–MuCulloch, 1927: 57 (in parts, the headwater of some northern streams).

Oligorus mitchelli.–Macleay, 1887: 981, 982 (in part, specimen from Richmond River).

Maccullochella macquariensis.–Whitley, 1937: 126 (in part, Richmond and Clarence systems).–Lake, 1959: 5 (in part, 2 coastal rivers – the Richmond and Clarence).–Lake, 1967: 31 (in part, in a few coastal streams in northern NSW).–Roughley, 1968: 133 (in part, headwaters of Richmond and Clarence Rivers).–Lake, 1971: 33 (in part, Clarence and Richmond Rivers).–Grant, 1987: 435 (in part, Clarence and Richmond Rivers).

Maccullochella peeli.–Berra & Weatherley, 1972: 60, 61 (in part, Clarence River).–Lake, 1978: 49 (in part, Clarence and Richmond Rivers).–MacDonald, 1978: 668 (in part, Clarence and Richmond Rivers).–Llewellyn & MacDonald, 1980: 143 (in part, Richmond and Clarence Rivers).–Pollard *et al.*, 1980: 246 (in part, Richmond and Clarence Rivers).–Llewellyn, 1983: 15 (in part, north coast rivers, possibly introduced).

Maccullochella sp.–Merrick & Schmida, 1984: 201 (Clarence River).–Harris, 1987: 8, 39 (coastal NSW rivers).–Allen, 1989: 138, 142, 143 (Clarence River system).–Ingram *et al.*, 1990: 179, 180 (Clarence River system).–Pollard *et al.*, 1990: 74 (eastern freshwater cod).

Maccullochella ikei Rowland, 1986: 16,17 (Clarence River system).

Maccullochella ikei.–Rowland, 1985 (unpublished): iv, 23-66 (Clarence River system).–Rowland, 1988b: 18, 19, 20, 22 (Clarence River system).–Rowland, 1988c: 168, 170 (some southern tributaries of the Clarence River system).–Hoser, 1991: 60 (Clarence River system).

Type material. LECTOTYPE, AMS I.31090-001, 410 mm, female, NSW, Nymboida River, at junction with Mann River (29°39'S 152°30'E), granite rocks and gravel to 4 m, angled, K. Clark, 21 Nov. 1984. PARALECTOTYPES, QM I27990, 422 mm, female, Mann River, 2 km upstream of junction with Nymboida River (29°38'S 152°29'E), 1 m, angled, R. Cockbain, 8 June 1982; AMS I.31089-001, 385 mm, female, same location as lectotype, angled, R. Lockwood, 21 Nov. 1984; 503 mm, female, same location as

lectotype, angled, C. Graham, 31 Sept. 1981 (specimen lost).

Other material. AMS I.31090-002, 2: 407-410 mm, males, Mann River, 6 km upstream of Jackadgery (29°37'S 152°33'E), gill net, S. Rowland, 12 Apr. 1986; AMS I.31090-001, 2: 305-320 mm, immature, same location as lectotype, gill net, S. Rowland, 13 Apr. 1986; QM I27991, 395 mm, female, Nymboida River, Ramornie State Forest (29°43'S 152°34'E), 2 m, angled, G. Stewart, 7 Apr. 1987; QM I27992, 355 mm, female, same locality as lectotype, gill net, S. Rowland, 27 Sept. 1987; AMS I.31092-001, 355 mm, female Nymboida River, Buccarumbi (29°51'S 152°35'E), 3 m, angled, F. Prokop, 4 May 1988; AMS I.31093-001, 2: 375-456 mm, males, same location as preceding, 1-3 m, angled, F. Prokop & G. Stewart, 18 May 1988; QM I27993, 440 mm, male, same location as preceding, 2 m, angled, K. Clark, 3 Aug. 1988.

Other specimens. These were examined live in the field and released or disposed of (18: 215-515 mm), as for lectotype, paralectotypes and other material.

Diagnosis. A species of freshwater cod, *Maccullochella*, differing from *M. p. peelii* by having longer pelvic fins, larger orbit length, larger and morphologically distinct sagittal otoliths, and distinctive colouration, from *M. p. mariensis* by the combination of a narrower caudal peduncle, shorter post-orbital head length, larger orbit, shorter inter-orbital width, more scale rows below the lateral line, longer fifth/sixth dorsal spine, and greater extension of the first anal pterygiophore towards the vertebral column, and from *M. macquariensis* by having a concave head profile, protruding lower jaw, 15 precaudal vertebrae, greater extension of the first anal pterygiophore towards the vertebral column and distinctive colouration.

Description. Details of morphometrics of the lectotype, paralectotypes and other material and specimens are given in Table 10.

Dorsal fin XII, 14 (X-XII, 13-16); anal fin III, 12 (III, 11-12); pectoral fin rays 17 (16-19); pelvic fin I, 5; caudal fin rays 18 (17-19); predorsal bones 2 (2-3); precaudal vertebrae 15 (15); caudal vertebrae 20 (20).

Large, elongate, deep-bodied fish; slightly compressed. Depth from dorsal origin to base pelvic fin 28.3 (26.0-30.3)% SL. Body dorsal profile convex, highest above pectoral base. Caudal peduncle elongated, 19.8 (19.8-24.8)% SL.

Head broad, width 62.1 (46.0-66.2)% HL; moderately compressed; profile distinctly concave. Lower jaw protruding beyond upper; mouth large, gape extending to posterior border of eye. Eyes moderately large, dorsolateral; orbit length 14.3 (12.0-19.0)% HL. Irregular rows of villiform, curved teeth in jaws, on vomer and palantines. Operculum with fleshy margin; 2 spines, lower spine largest. Edge of preoperculum smooth.

Lateral line distinct, following dorsal profile, extending to base of caudal fin; 70 (65-82) scales in lateral line. Body covered by small scales, mostly ctenoid; cheeks and opercular scaled, snout naked.

Pelvic fin inserted in advance of pectoral base; first ray elongated into 2 filaments, second long, tapering to fine tip; pelvic fin 17.9 (16.6-21.0)% SL. Pectoral fin large, 16.7 (14.2-19.0)% SL; upper rays longest. Dorsal fin origin posterior to pectoral and pelvic bases. Dorsal spines strong, fifth-sixth longest 10.8 (8.5-13.0)% SL; soft dorsal fin rounded. Anal fin opposite soft dorsal, rounded; second spine largest. Caudal fin large, rounded.

Colour in life and in alcohol. In life yellow-green to golden with black to very dark green, heavily reticulated mottling on dorsal surface, head and sides, extending onto ventral surface in some specimens. Ventral surface of head and body dark grey; becoming grey-white when in turbid water (Fig.4). Dorsal, pectoral, caudal and anal fins clearish to very dark grey-green with mottling on their bases. Thin pale-grey to whitish margins sometimes present on soft dorsal, anal and caudal fins. Pelvic fin colourless, translucent; filaments white.

In alcohol, grey dorsally with black to dark grey heavily reticulated mottling on dorsal surface, head and sides; ventral surface grey and brownish. Fins dark to grey; pelvic fin white.

Species can attain a large size and cod of 22.7 to 27.3 kg were frequently caught in the Clarence system (Wilcox, 1863); largest specimen reported 41 kg from Koreelah Creek in 1921 (K. Murphy, personal communication).

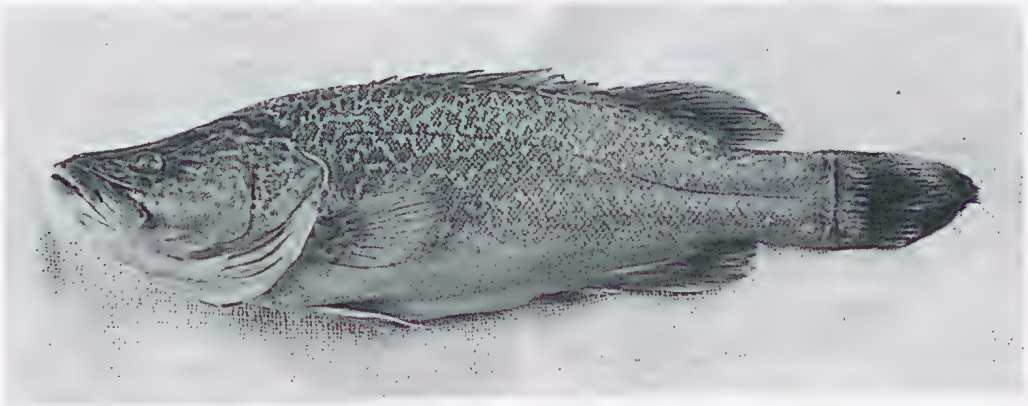

Fig.7. *Maccullochella ikei*. Lectotype (AMS I.31090-001), 410 mm SL (photograph, Kevin Clark).

Etymology. Named *ikei* after the author's late grandfather, Isaac (Ike) Morgan Rowland, who was a great admirer and angler of Australian native inland fishes, in particular Murray cod.

Remarks. No types were listed in the original species description (Rowland, 1986). The type series includes all those specimens from which data were taken as listed in the unpublished thesis of Rowland (1985); the lectotype and paralectotypes are the remaining extant specimens from that syntypic series. Other material includes the specimens collected since 1985.

The population of cod in the Mary system is morphologically and genetically distinct from the other species of *Maccullochella*. The data suggest that this population is more similar to *M. p. peelii* than *M. ikei*, and pending breeding studies and further investigation of the evolutionary relationships within *Maccullochella*, is here described as a subspecies of *M. peelii*.

Maccullochella peelii mariensis n.subsp.

Mary River cod

Fig.4

Oligorus macquariensis.–Ogilby, 1893: 19 (in part, Mary River).–Ogilby, 1895: 71, 72 (in part, Mary River).–McCulloch & Whitley, 1925: 102 (in part, Mary River).

Maccullochella macquariensis.–Whitley, 1937: 128 (in part Mary River).–Roughley, 1968: 133 (in part, Mary River).–Lake, 1971: 33 (in part, Mary River).–Grant, 1982: 785 (in part, Mary and Dawson Rivers).–Grant, 1987: 435 (in part, Mary and Dawson Rivers).

Maccullochella peeli.–Berra & Weatherley, 1972: 60 (in part, Mary River).–Lake, 1978: 49 (in part Mary River).–Llewellyn & MacDonald, 1980: 143 (in part, Mary and Dawson Rivers).

Maccullochella sp.–Merrick & Schmida, 1984: 202 (Mary River system).–Harris, 1987: 9, 39 (Mary River).–Rowland, 1988c: 171 (Mary River system).–Allen, 1989: 142 (Mary River).–Ingram *et al.*, 1990: 179, 180 (Mary River system).–Pollard *et al.*, 1990: 74 (Mary River).

Type material. HOLOTYPE, QM I27994, 382 mm, female, Queensland, Tinana Creek, Bungawatta Station (25°48'S 152°42'E), clay, mud and timber to 3 m, angled, R. Cockbain, 9 Feb. 1984. PARATYPES, QM I27995, 476 mm, female, Coondoo Creek (26°00'S 152°50'E), angled, G. Cook, Dec. 1983; QM I27996, 555 mm, male, Coondoo Creek (26°00'S 152°50'E), gill net, S. Rowland, 7 Feb. 1984; QM I27997, 417 mm, female, same locality as preceding, gill net, S. Rowland, 8 Feb. 1984; QM I27998, 235 mm, immature, Six-mile Creek, 10 km upstream of junction with Mary River (26°16'S 152°45'E), angled, C. Graham, 8 Feb. 1984; AMS I.32345-001, 440 mm, female, same data as QM I27997; AMS I.32346-001, 387 mm, male, Six-mile Creek, same locality as QM I27998 angled, J. Rowland, 9 Feb. 1984; AMS I.32347-001, 464 mm, female, same locality as preceding, angled, C. Graham, 9 Feb. 1984.

Diagnosis. A subspecies of *Maccullochella peelii* distinguished from the nominal subspecies by the combination of longer pelvic fins, deeper and shorter caudal peduncle, shorter extension of first anal pterygiophore towards vertebral column, larger sagittal otoliths and distinctive colouration, from *M. ikei* by the combination of deeper caudal peduncle, greater postorbital head length, smaller orbit, larger interorbital width, fewer scale rows below lateral line, shorter fifth-sixth dorsal spine and shorter extension of the first anal pterygiophore, and from *M. macquariensis* by having concave head profile, protruding lower jaw, 15 precaudal vertebrae and distinctive colouration.

Description. Details of morphometrics are given in Table 7. Similar general shape to *M. p. peelii* and *M. ikei* but with following details.

Dorsal fin XI, 15; anal fin III, 13 (III, 12-13); pectoral fin rays 18 (19-20); pelvic fin I, 5; caudal fin rays 18 (16-18); predorsal bones 2 (2-3); precaudal vertebrae 15; caudal vertebrae 19 (19-20).

Depth from dorsal origin to base pelvic fin 31.6 (28.3-33.6)% SL. Caudal peduncle elongated 19.3 (19.0-21.4)% SL and relatively deep 13.5 (12.3-14.2)% SL.

Head width 65.0 (47.8-64.6)% HL; orbit length 13.9 (10.0-13.8)% HL.

Lateral line scales 67 (68-74); pelvic fin 18.4 (16.4-19.8)% SL; pectoral fin 18.3 (16.5-19.3)% SL; fifth-sixth dorsal spine longest 9.3 (6.1-9.8)% SL.

Colour in life and alcohol. In life yellowish to pale green with dark heavily reticulated mottling on dorsal surface, head and sides, extending onto ventral surface in some specimens. Ventral surface of head and body grey-green to whitish. Dorsal, pectoral, caudal and anal fins clearish to dark with grey-green mottling on their bases. Thin whitish margins on soft dorsal, anal and caudal fins. Pelvic fin colourless to whitish; filaments white.

In alcohol, grey dorsally and grey-brown on sides with dark reticulated mottling on dorsal surface, head and sides; ventral surface grey-brown. Fins dark to grey-brown; pelvic fin white.

Subspecies can attain a large size and reported to grow to 23.5 kg (Merrick & Schmida, 1984).

Etymology. Named *mariensis* after the Mary River in which the new subspecies is endemic.

Key to the Species of *Maccullochella* in South-eastern Australia

1. Head profile straight. Upper jaw overhangs lower jaw. Blue-grey dorsally with speckled pattern of dark grey to black spots and small bars dorsally and laterally. Precaudal vertebrae 14 ..... *Maccullochella macquariensis*

—— Head profile concave. Jaws equal or lower jaw protruding. Distinct mottled pattern dorsally and laterally. Precaudal vertebrae 15 2

2. Cream to olive to yellow-green with pale to dark green reticulated mottling dorsally and laterally sometimes with small dark spots between reticulation; ventral surface white to creamy-white. Whitish, relatively short pelvic fin 13.2-16.4% standard length. Orbit length 9.7-12.9% head length. Anal rays 12-15. Otolith with prominent antirostrum; otolith length 2.5-2.9% total length ..... *Maccullochella peelii peelii*

—— Pale green to yellow-green to golden with black to very dark green, heavily reticulated mottling dorsally and laterally, sometimes extending onto ventral surface; ventral surface dark grey to whitish. Clear, relatively long pelvic fin 16.4-20.7% standard length. Otolith with small antirostrum; otolith length 2.9-3.5% total length 3

3. Depth caudal peduncle 12.3-14.2% standard length. Orbit length 10.0-13.8% head length. Interorbital width 25.1-30.4% head length. Scale rows below lateral line 30-34. Fifth/sixth dorsal spine 6.1-9.8% standard length. Anal rays 12-13. First anal pterygiophore length 79-86% distance from its base to first caudal vertebra. Otolith length 2.9-3.3% total length ..... *Maccullochella peelii mariensis*

—— Depth caudal peduncle 10.7-12.5% standard length. Orbit length 12.0-19.0% head length. Interorbital width 20.8-27.5% head length. Scale rows below lateral line 32-52. Fifth/sixth dorsal spine 8.5-13.0% standard length. Anal rays 11-12. First anal pterygiophore length 89-97% distance from its base to first caudal vertebra. Otolith length 3.2-3.5% total length ..... *Maccullochella ikei*

Discussion

Although the relationship between allopatric populations can be difficult to determine, the technique of electrophoresis enables a quantitative analysis of genetic divergence, and when coupled with morphological techniques, information on taxonomic, and phylogenetic relationships between populations is maximised (Hillis, 1987). The values of the coefficients of genetic identity and genetic distance between *M. p. peelii* and *M. ikei* (I=0.72; D=0.33) and between *M. ikei* and *M. p. mariensis* (0.73; 0.32) are consistent with values previously reported between congeneric species of fishes (Avise, 1974; Ayala, 1975; Shaklee & Tamaru, 1981; Shaklee *et al.*, 1982). The species-specific banding patterns of *Mpi-1, Idh-2, Iddh-1, Gpi-A*$_2$ and *G3pdh-1*, liver esterases, and the muscle general protein, as well as the morphometric differences and the abnormalities and inviability of hybrid larvae provide strong evidence of the divergence and evolution of reproductive isolation between cod from the Murray-Darling and Clarence systems.

The 'subspecies' taxon is generally used to arbitrarily identify geographically isolated populations that have undergone some morphological and/or genetic change (Dobzhansky, 1970; Frankel & Soulé, 1981). The cod population in the Mary system is genetically and

morphologically distinct from both *M. p. peelii* and *M. ikei*. Although the phenotypes of muscle general protein (Fig.2) and the character length of pelvic fin suggest a closer relationship to *M. ikei*, the coefficient of genetic identity with *M. peelii* of 0.85 is in the range (0.80-0.96) normally associated with subspecies of fish (Avise, 1974; Avise & Smith, 1977; Philipp *et al.*, 1983; Crabtree & Buth, 1987; Leary *et al.*, 1987). Overall, the genetic and morphometric data suggest a closer relationship to *M. p. peelii*, hence the description of cod in the Mary system as *M. p. mariensis*. The two distinct forms of cod in this system that are recognised by fishermen (Merrick & Schmida, 1984) were not identified in the current study.

It is hypothesised that the cod of the western drainage was the ancestral stock from which founders of *M. ikei* and *M. p. mariensis* become geographically isolated. Fossil Murray cod of Miocene Age (26-7 million years ago [mya]) have been found in the Warrumbungle Mountains and Cooma regions (Hills, 1946; Taylor *et al.*, 1980). Diatom flora associated with some of these fossils is of the type found with lower Tertiary basalts (Gill, 1970) and so ancestral *Maccullochella* may be up to 60-65 m y old (Rowland, 1989).

The genetic distances and the estimated times of divergence (1.7-0.8 mya) suggest that the vertical uplift associated with the formation of the Great Dividing Range (GDR) was not responsible for the geographic isolation of cod in the eastern drainage. Most of the earth movements which formed the Eastern Highlands took place before the Miocene (Ollier, 1978) and the GDR assumed its present gross character early in the Cainozoic Era which commenced 65 mya (Jones & Veevers, 1980). The westward migration of the dividing range has resulted in complex, large-scale stream capture and short, steep coastal rivers have been successively capturing the headwaters of westerly-flowing streams (Herbert, 1980). The founder populations of *M. ikei* and *M. p. mariensis* could have become isolated in the eastern drainage, during this process of stream capture, as was first suggested by McCulloch (1914) to explain the presence of 'Murray cod' in north-eastern NSW and south-eastern Queensland. Speciation can be very rapid in small founder populations (Mayr, 1982) and the vastly different types of habitats in the coastal river systems compared to the western drainage could have contributed to rapid divergence and speciation. An alternative hypothesis is that cod have made separate invasions of Australian freshwaters from marine environments east and west of the GDR, as has been suggested for some atherinids by Crowley (1990).

Although conspecific populations have been recorded east and west of the GDR (Crowley, 1990) in other species of fish, two previous studies have also identified separate species. Crowley *et al.* (1986) found that the rainbowfish of the coastal systems of northern NSW and southern Queensland is *Melanotaenia duboulayi*, whereas *M. fluviatilis* is confined to the Murray-Darling system, and Dufty (1986) suggested that eastern and western populations of Macquarie perch (*Macquaria australasia*) are separate species. The findings of these, plus the current study suggest that the GDR has played a role in the speciation of some freshwater fishes in eastern Australia. There is clearly a need to maintain the integrity of native fish faunas within drainages, particularly where there is doubt about the taxonomic and reproductive relationships between populations.

Past and present distribution and abundance of cod in the eastern drainage. Historical reports of the 1800s and early 1900s indicate that large populations of cod were once present in each of the Clarence, Richmond, Brisbane and Mary systems. When the Clarence Valley was first settled in the 1830s, cod were plentiful in all the freshwater reaches of the Clarence River and its tributaries (Bawden, 1888) and fish up to 27.3 kg were frequently caught in the Clarence and Orara Rivers (Wilcox, 1863). Many of the very early settlers "lived off the land" and caught cod and other fish and native animals for food (Wilkinson, 1981). In a letter dated Grafton, 10 May 1866, the distinguished naturalist John MacGillivray wrote of catching 25 cod up to 22.7 kg during a trip to the Wymboida [sic] River (Beaton, 1868). Early settlers who were mainly cedar cutters, found that cod up to 27.3 kg were plentiful in the Richmond River and many of its tributaries (Bundock, 1898; S. King, R. Russ, personal communication). In 1824, the explorers John Oxley and Allan Cunningham recognised a fish that had been caught from the Brisbane system by an old Aborigine, as the cod found in the western rivers (McMinn, 1970). There were numerous reports about the relative abundance of what were presumed to be Murray cod in the upper Stanley River, a major tributary of the Brisbane River, during the early 1900s (Stephenson, 1953) and cod were so plentiful in the Brisbane and Mary systems during the early 1900s that some settlers used them as pig feed (J. Winkel, personal communication).

There has been a dramatic reduction in the distribution and abundance of cod in the eastern drainage and cod were probably extinct in the Brisbane and Richmond systems by the end of the 1930s. Only a few cod were reported from the Stanley River in the 1940s (Stephenson, 1953) and there has not been an authenticated report of cod from any location in the Brisbane system since that time (S.H. Midgley, R. McKay, personal communication). A marked decline of cod in the Richmond River occurred after 1926 when the north coast railway, which closely follows the river, was constructed north of Casino. Elderly, local residents claim that the river was extensively dynamited during the construction of the railway (B. Wilson, personal communication), and this, plus several very large fish kills involving many cod during heavy flooding in the 1920s and 1930s (D. Machin, S. King, personal communication) were probably the major factors in the demise of cod in this system. The last authenticated capture of a cod from the Richmond system was in 1971 (J. Bell, personal communication).

There has been a decline in the number of cod in

the Mary system since the early 1900s (S.H. Midgley, J. Winkel, K. Passlow, personal communication) and the population in this system is now restricted mainly to Six-mile, Tinana, Coondoo, Widgee, Station and Oby Oby Creeks. Cod are not common in the Mary River where the clearing of timber from the river and its banks for agricultural development has led to extensive siltation and loss of in-stream cover (S.H. Midgley, personal communication).

Cod disappeared from much of the Clarence system after a number of massive fish kills during the late 1920s and the 1930s. Long dry periods, followed by extensive bushfires and then heavy summer rains preceded some of the fish kills (S. Adams, K. Murphy, F. Winters, personal communication). Such conditions have been reported to cause a deterioration of water quality, including a marked depletion of dissolved oxygen, and increased turbidity, concentration of suspended solids, electrical conductivity and nutrient levels in some Australian rivers (Chessman, 1986). In addition, releases of contaminated water from the tailings dams at gold and tin mines are also thought to have caused the death of cod and other freshwater fish in parts of the Clarence system (F. Winters, personal communication).

Cod are now very rare or absent in the major northern tributaries of the system, the Clarence, Rocky and Cataract Rivers and they are no longer found in the Orara River, where they were once very common (Wilcox, 1863). The north coast railway, in part, closely follows the Orara River from Coffs Harbour to Grafton and dynamiting may have also been responsible for the rapid decline of cod in this river. Parts of the catchments of these rivers have undergone some agricultural development and this may have contributed to a loss of cod habitat. Since the late 1960s small numbers of cod (usually less than 5 kg) have been caught

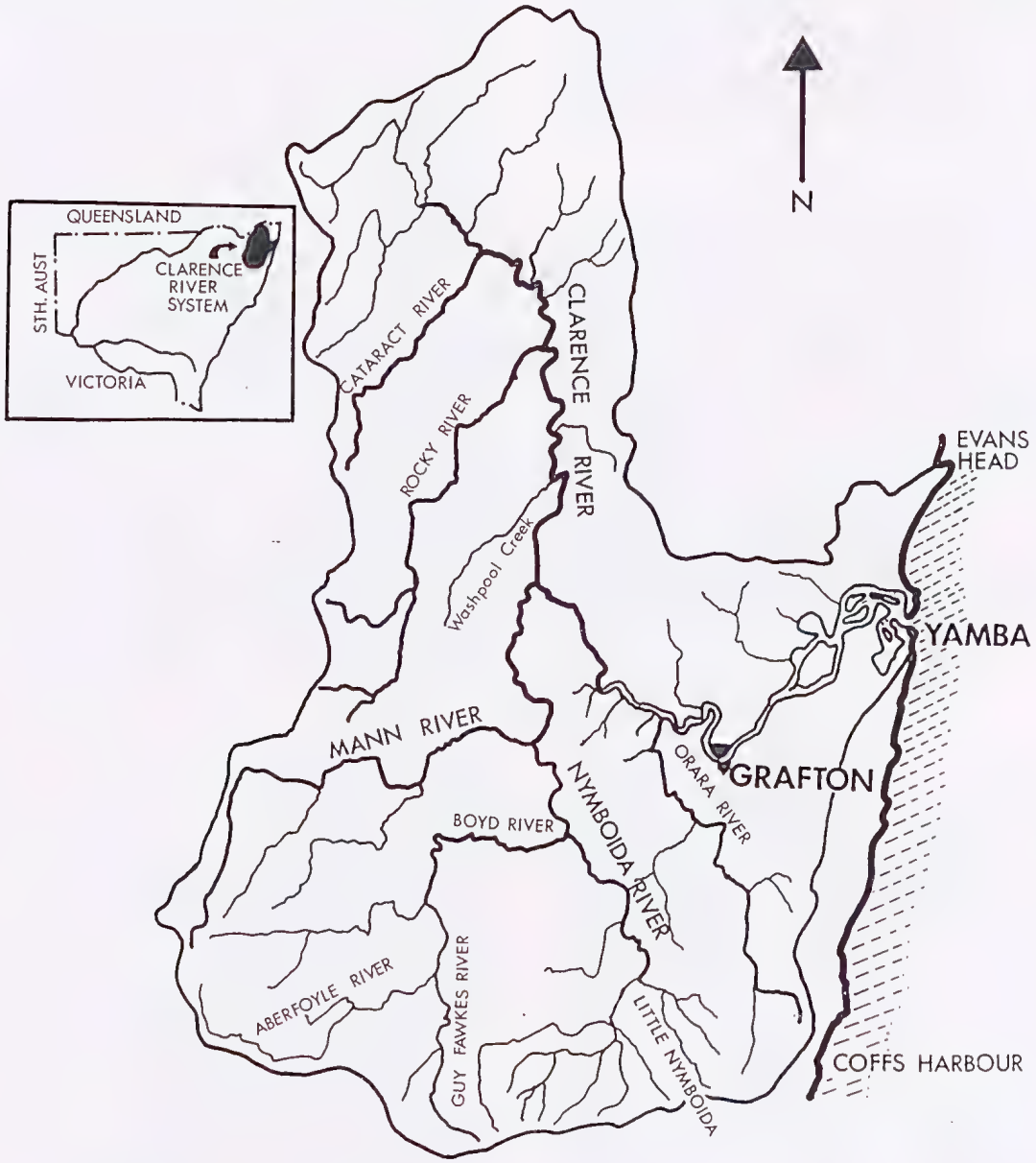

Fig.8. The Clarence River system, NSW.

only from tributaries such as the Nymboida, Little Nymboida, Boyd and Mann Rivers (Fig.8), where some pristine habitat still exists.

Maccullochella ikei and *M. p. mariensis*, like other species of *Maccullochella*, are large, long-lived, slow-growing species, with relatively low fecundity and a long generation period (Rowland, 1985). An extended age distribution in such fishes represents an evolutionary adaptation by which potentially high larval mortality in unfavourable breeding seasons is compensated for by repeated annual spawnings over the life span of individuals (Giesel, 1976; May, 1976). It is possible that *M. ikei* and *M. p. mariensis* have lost this advantage and that the intrinsic biology of these species has prevented their recovery from the low population levels caused by the fish kills and other factors. In addition, these species are potentially threatened by overfishing, pollution, habitat destruction or degradation, including the deterioration of water quality, the introduction of fishes not native to the eastern drainage (including possible hybridisation with hatchery-reared Murray cod), disease, the loss of genetic variability, and inbreeding. Small, isolated populations are extremely susceptible to extinction (Frankel & Soulé, 1981).

***Maccullochella ikei*, an endangered species.** The eastern freshwater cod is now classified as endangered (Harris, 1987; Ingram *et al.*, 1990). In an effort to conserve *M. ikei*, there is a prohibition on the capture of freshwater cod, *Maccullochella* spp. from waters north of the Macleay River to the Queensland border, and the Eastern Freshwater Fish Research Hatchery has been constructed at Grafton so that techniques for the artificial breeding of *M. ikei* can be developed. Guidelines for the genetically-sound production and stocking of Australia's endangered and threatened fishes have been established (Rowland & Barlow, 1988) and the successful restocking of the Richmond and Clarence Rivers systems with hatchery-reared fry will reduce the vulnerability of *M. ikei* to the factors which cause extinction.

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APPENDIX

Table 1. Number and standard length of cod from each sampling site.

River system	Sampling sites	No. of cod sampled	Standard length range (mm)
Murray-Darling	Gwydir River (near Bingara) and MacIntyre River (Elsmore)	10	375-495
	Murray River (Lock 15), Edwards River (Stevens Weir) and Wakool River (Wakool)	15	355-520
	Farm dams near Narrandera	12	242-510
	Lake Mulwala	8	530-680
Clarence	Within 32 km of the junction of the Mann and Nymboida River	18	212-515
	as above	14[a]	305-456
Mary	Six-mile, Coondoo and Tinana creeks	9	235-555

[a] lectotype, paralectotypes and other material.

Table 2. Details of electrophoretic systems.

System	Medium	Buffer	Running conditions		
			voltage (V)	current (mA)	time (h)
A	polyacrylamide	discontinuous LiDH[a]	1500	40	3
B	starch	Tris maleate (pH 7.4)	50	40	15.5
C	starch	as above	60	50	6.5
D	starch	Tris borate EDTA (pH 8.6)	100	25	19
E	starch	Lithium borate-tris citrate (pH 8.2; pH 6.6)	220	–	3
F	cellulose acetate	Tris borate EDTA (pH 8.6)	200	–	1.5

[a] after Keenan & Shaklee (1985).

Table 3. Proteins assayed, tissues examined, the number of loci found and the number of cod examined in the electrophoretic analysis. E.s. = Electrophoretic system; *M.p.p.* = *Maccullochella peelii peelii*; *M.i.* = *Maccullochella ikei*; *M.p.m.* = *Maccullochella peelii mariensis*.

Protein	EC No.	Abbreviation	E.s.	Tissue	No. loci	No. cod analysed		
						*M.p.p.**	*M.i.*	*M.p.m.*
Phosphoglucomutase	5.4.2.2	PGM	B	Muscle	1	8	6	6
Fumarase	4.2.1.2	FUM	C	Muscle	1	8	6	6
Lactate dehydrogenase	1.1.1.27	LDH	C	Muscle	1	8	6	6
Malate dehydrogenase	1.1.1.37	MDH	C	Muscle	2	8	6	6
Aldolase	4.1.2.13	ALD	F	Liver	1	5	5	–
Superoxide dismutase	1.15.1.1	SOD	D	Liver	1	8	4	8
Aspartate aminotransferase	2.6.1.1	AAT	D	Liver	2	8	4	8
Glutamate dehydrogenase	1.4.1.3	GLUDH	F	Liver	1	5	5	–
Mannose-6-phosphate isomerase	5.3.1.8	MPI	B	Muscle	1	13	12	6
Isocitrate dehydrogenase	1.1.1.42	IDHP	B	Muscle	2	13	12	–
Malate dehydrogenase ($NADP^+$)	1.1.1.40	MDH(NADP)	E/F	Muscle	1	15	8	8
L-iditol dehydrogenase	1.1.1.14	IDDH	F	Liver	2	11	11	6
Glucose-6-phosphate isomerase	5.3.1.9	GPI	C	Muscle	2	13	11	6
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3PDH	D/E	Muscle	1	5	4	6
Glucose-6-phosphate dehydrogenase	1.1.1.49	G6PDH	F	Liver	2	9	7	4
Esterases	3.1.1.2	EST	B	Liver	?	5	5	–
General protein	–	–	A	Muscle	?	12	5	8

* includes specimens from each sampling site.

Table 4. Allele frequencies at loci of diagnostic enzymes in species of *Maccullochella*.

Locus	Allele	*M. p. peelii*	*M. ikei*	*M. p. mariensis*
Mpi-1	100	1.00	–	1.00
	87	–	1.00	–
Idh-1	100	1.00	1.00	1.00
Idh-2	100	–	1.00	no data
	75	1.00	–	
Iddh-1	100	1.00	–	0.17
	88	–	1.00	0.83
Iddh-2	100	1.00	1.00	1.00
Gpi-A_2	100	1.00	–	1.00
	92	–	1.00	–
G3pdh-1	100	–	1.00	–
	90	1.00	–	1.00
G6pdh-1	100	0.14	0.32	0.44
	92	0.38	0.05	–
	83	0.05	0.32	0.33
	69	0.38	–	0.22
	58	0.05	0.32	–

Table 5. Coefficients of genetic identity (I) and the genetic distances (D) between species of *Maccullochella*.

Cod	I	D
M. p. peelii; *M. ikei*	0.72	0.33
M. p. peelii; *M. macquariensis*	0.79[a]	0.24[a]
M. p. peelii; *M. p. mariensis*	0.85	0.16
M. ikei; *M. p. mariensis*	0.73	0.32

[a] Data from MacDonald (1978).

Table 6. Morphometric characters of *M. p. peelii* from Lake Mulwala.

Character	No.	Range	Mean	S.D.	t
% STANDARD LENGTH					
body depth I	6	30.3-37.0	32.2	2.50	4.22**
body depth II	5	28.5-29.5	28.8	0.43	0.68
peduncle depth	8	11.7-13.7	12.5	0.70	4.08**
peduncle length	8	20.3-23.3	21.5	0.92	0.69
predorsal length	8	40.8-43.5	42.1	0.91	3.53*
dorsal base	8	44.5-47.1	46.5	0.89	2.92*
anal base	8	16.1-18.7	17.5	0.77	1.11
pectoral fin	8	16.3-17.7	16.7	1.14	0.50
pelvic fin	8	13.0-15.5	14.6	0.76	0.82
head length	8	31.5-35.0	32.9	1.04	2.44
% HEAD LENGTH					
head width	3	47.0-51.9	48.9	2.67	3.14*
snout length	8	27.0-28.8	28.0	0.63	3.09*
post-orbital length	8	57.5-64.6	62.3	2.23	1.47
upper jaw length	8	43.0-46.5	45.3	1.24	0.10
inter orbital width	8	22.8-29.4	26.4	2.26	0.36
inter nare width	8	22.3-24.2	23.4	0.68	1.61
MERISTICS					
dorsal spines	8	11-12	11.4	0.52	0.94
dorsal rays	8	14-16	14.9	0.64	2.05
anal rays	8	12-13	12.6	0.52	0.31
pectoral rays	8	19-20	19.6	0.52	1.71
gill rakers	7	16-18	17.3	0.76	1.95
lateral line scales	6	72-86	79.3	6.38	3.76**
scale rows above	6	23-26	24.3	1.03	1.21
scale rows below	6	32-38	35.3	2.50	0.78
pyloric caecae	7	4	4.0	–	0
caudal rays	8	17-19	17.9	0.84	0.57

t – Student's t-test comparison of means with *M. p. peelii* from rivers and farm dams. ** significant P<0.001; * significant P<0.01; others not significant P>0.01.

Table 7. Comparison of morphometric characters between *M. p. peelii* (ex rivers and farm dams), *M. ikei* and *M. p. mariensis*.

Character	*M. peelii*					*M. ikei*					*M. p. mariensis*				
	No.	Range	Mean	S.D.	t^a	No.	Range	Mean	S.D.	t^b	No.	Range	Mean	S.D.	t^c
% Standard Length															
body depth (I)	22	27.2-31.6	29.1	1.29	0.30	4	27.3-30.2	28.9	1.23	1.85	9	28.3-33.1	30.5	1.49	2.57
body depth (II)	32	25.3-33.8	28.1	2.08	0.98	16	26.1-30.9	28.7	1.74	1.32	9	27.1-32.8	29.8	2.17	2.08
peduncle depth	37	10.3-13.0	11.4	0.66	0.39	18	10.7-12.6	11.5	0.55	7.35**	9	12.3-14.2	13.2	0.59	7.33**
peduncle length	37	19.8-23.3	21.8	1.00	0.94	18	20.0-24.8	22.1	1.36	3.33*	9	19.0-21.4	20.4	0.69	3.77**
predorsal length	36	36.8-42.5	40.3	1.35	0.04	18	36.7-43.1	40.2	1.86	0.44	9	38.5-43.1	40.5	1.34	0.58
dorsal base	35	42.4-47.9	45.1	1.29	3.23*	18	40.1-47.2	43.7	1.81	2.81*	9	44.1-47.2	45.5	0.85	0.89
anal base	37	16.4-21.0	17.9	1.02	5.40**	18	15.1-17.5	16.4	0.65	1.08	9	14.7-18.6	16.9	1.32	2.50
pectoral fin	37	14.7-18.1	16.8	0.81	2.96*	17	15.8-19.0	17.5	0.79	0.14	9	16.5-19.3	17.5	0.94	2.12
pelvic fin	37	13.2-16.4	14.9	0.86	13.49**	17	16.9-19.5	18.4	0.90	0.41	9	16.4-19.8	18.2	1.19	9.85**
dorsal spine (5th/6th)	37	6.5-12.5	8.7	1.64	3.33*	17	8.5-13.0	10.2	1.17	4.02**	9	6.1-9.8	8.3	1.04	0.68
head length	37	30.3-34.5	32.0	0.98	2.97*	18	31.7-36.7	32.9	1.22	0.39	9	31.8-34.3	33.0	0.75	3.11*
% Head Length															
head width	29	40.9-68.0	57.4	4.45	0.08	15	46.0-63.5	57.3	5.24	0.14	9	47.8-64.6	57.6	5.57	0.12
snout length	40	26.5-30.5	29.0	0.91	0.98	18	27.9-30.6	29.3	0.87	0.36	9	27.8-30.3	29.2	0.86	0.24
post-orbital length	39	56.9-64.9	61.3	1.71	7.50**	18	54.7-59.7	57.9	1.31	3.94**	9	57.8-61.5	59.9	1.12	2.40
orbit	25	9.7-12.9	10.9	0.67	11.56**	18	12.8-19.0	14.6	1.41	4.66**	9	10.0-13.8	12.0	1.23	3.46*
upper jaw length	40	41.0-48.4	45.2	1.84	2.54	18	42.8-48.9	46.5	1.56	1.24	9	38.9-49.3	45.5	2.91	0.28
inter orbital width	39	23.6-29.6	26.7	1.67	4.40**	18	20.8-27.5	24.6	1.57	4.54**	9	25.1-30.4	27.7	1.88	1.62
inter nare width	39	21.0-24.9	22.8	0.96	0.23	17	21.4-24.4	23.0	0.72	1.24	9	22.4-25.3	23.4	1.02	1.69
Meristics															
dorsal spines	37	11-12	11.2	0.42	1.14	18	10-12	11.1	0.64	0.27	9	11	11.0	–	1.57
dorsal rays	36	14-16	15.3	0.54	3.33*	18	14-16	14.8	0.52	0.97	9	15	15.0	–	1.83
anal rays	37	12-15	12.5	0.77	5.50**	18	11-12	11.4	0.51	4.24**	9	12-13	12.3	0.50	0.78
pectoral rays	37	18-21	19.1	0.91	3.67**	18	16-19	18.2	0.79	3.39*	9	18-20	19.2	0.67	0.53
gill rakers	32	16-20	18.1	1.03	1.13	14	18-20	18.4	0.65	0.42	8	17-21	18.6	1.60	1.17
lateral line scales	35	66-80	72.1	3.95	1.08	18	65-82	73.4	4.72	1.73	9	68-74	70.6	2.30	1.12
scale rows above	37	22-34	25.9	3.04	2.79*	17	19-28	23.5	2.65	0.82	9	23-26	24.2	1.09	1.60
scale rows below	37	29-50	37.4	6.37	1.81	18	32-52	40.5	4.81	4.89**	9	30-34	32.4	1.51	2.31
caudal rays	36	15-20	17.6	1.10	0.57	17	17-19	17.5	0.72	1.29	9	16-18	17.1	0.60	1.40

t – Student's t-test; t^a – *M. p. peelii* vs *M. ikei*; t^b – *M. ikei* vs *M. p. mariensis*; t^c – *M. p. peelii* vs *M. p. mariensis*.
** significant P<0.001; * significant P<0.01; others not significant P>0.01.

Table 8. Osteological characters of *Maccullochella* spp. as determined from x-rays. Number of specimens examined in parentheses.

Character	*M. p. peelii* (3)	*M. ikei* (4)	*M. p. mariensis* (5)	*M. macquariensis* (3)
predorsal bones	3-4	2-3	2-3	2-3
precaudal vertebrae	15	15	15	14
caudal vertebrae	20	20	19-20	21
first anal pterygiophore[a] (%)	86-97	89-97	79-86	74-79

[a] length of first anal pterygiophore expressed as a percentage of the distance from the base of this pterygiophore to the ventral surface of the first caudal vertebra.

Table 9. Results of the cross-breeding experiment between Murray cod (MC) and eastern freshwater cod (EFC). Milt from two male Murray cod was used to fertilise the eggs stripped from the three females which ovulated.

Female	Weight (kg)	Oocyte diameter before injection (mm)	HCG (IU/kg)	Latent period (h)	Ovulation	No. of eggs	No. of larvae	Hatch rate (%)
EFC	1.35	2.6	500	48	–			
				55	–			
				68	–			
EFC	3.8	3.0	1000	47	–			
				48	–			
				56	–			
				68	–			
EFC	2.15	2.8	2000	46	+	6,750	147	2
				48	+	1,900	630	33
						8,650	777	9
MC	11.0	2.9	1000	48	+	27,200	675	3
				50	+	22,500	16,785	75
						49,700	17,460	35
MC	11.6	3.0	1000	4 8	+	29,000	16,910	58
				49	+	17,500	15,755	90
						46,500	32,665	70

Table 10. Morphometric characters of the lectotype, paralectotypes, other material and other specimens of *Maccullochella ikei*.

Character	Lectotype	Range: Paralectotypes (n=3)	Range: Other material (n=10)	Range: Other specimens (n=18)	*M. ikei* (n=32)
Standard length (mm)	410	385-503	305-456	212-515	
% STANDARD LENGTH					
body depth I	28.3	29.7-29.9	26.0-30.3	27.3-30.2*	26.0-30.3
body depth II	28.8	28.8-31.5	27.0-30.2	26.1-30.9*	26.1-31.5
peduncle depth	11.3	11.0-13.2	11.0-13.2	10.7-12.6	10.7-13.2
peduncle length	19.8	21.5-22.2	21.5-23.3	20.0-24.8	19.8-24.8
predorsal length	39.9	38.7-42.2	39.5-42.6	36.7-43.1	36.7-43.1
dorsal length	45.6	41.3-45.7	40.8-45.0	40.1-47.2	40.1-47.2
anal base	17.2	15.0-16.2	15.2-18.1	15.1-17.5	15.0-18.1
pectoral fin	16.7	17.4-18.1	14.2-18.5	15.8-19.0*	14.2-19.0
pelvic fin	17.9	17.2-19.4	16.6-19.7	16.9-21.0*	16.6-21.0
dorsal spine (5th/6th)	10.8	9.4-10.9	9.3-11.2	8.5-13.0*	8.5-13.0
head length	32.7	32.2-33.4	31.9-33.7	31.7-36.7	31.7-36.7
% HEAD LENGTH					
head width	62.1	59.3-65.9	58.8-66.2	46.0-63.5*	46.0-66.2
snout length	29.2	27.0-30.8	29.2-30.9	27.9-30.6	27.0-30.9
post-orbital length	57.1	56.2-57.5	56.6-59.4	54.7-59.7	54.7-59.7
orbit length	14.3	13.4-15.1	12.0-15.3	12.8-19.0	12.0-19.0
upper jaw length	47.1	47.4-47.7	40.3-51.1	42.8-48.9	40.3-51.1
inter orbital width	23.5	27.1-27.4	23.5-29.1	20.8-27.5	20.8-29.1
inter nare width	22.4	24.3-24.6	22.4-25.0	21.4-24.4*	21.4-25.0
MERISTICS					
dorsal spines	12	11-12	10-12	10-12	10-12
dorsal rays	14	13-15	13-15	14-16	13-16
anal rays	12	11	11-12	11-12	11-12
pectoral rays	17	17	17-19	16-19	16-19
gill rakers	–	–	–	18-20*	18-20
lateral line scales	70	68-71	65-80	65-82	65-82
scale rows above	23	24-25	25-30	19-28*	19-30
scale rows below	32	32-34	29-34	32-42	29-42
caudal rays	18	17-18	17-19	17-19*	17-19
predorsal bones	2	2-3	–	–	2-3
precaudal vertebrae	15	15	–	–	15
caudal vertebrae	20	20	–	–	20

* these data from 4-17 specimens (see Table 7).

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Atelomycterus fasciatus n.sp., a New Catshark (Chondrichthyes: Carcharhiniformes: Scyliorhinidae) from Tropical Australia

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ABSTRACT. A new atelomycterine catshark (Scyliorhinidae: Atelomycterinae), *Atelomycterus fasciatus* n.sp., is described from the continental shelf of northern Australia (North West Shelf, Arafura Sea, Gulf of Carpentaria and Torres Strait). It differs from *Atelomycterus marmoratus* (Bennett, 1830) and *A. macleayi* Whitley, 1939 in its longer snout, smaller, posteroventrally sloping dorsal fins, smaller anal fin, fewer small dark brown spots (sometimes absent), dark bands that occasionally encircle the tail, lower vertebral counts, and smaller size.

COMPAGNO, L.J.V. & J.D. STEVENS, 1993. *Atelomycterus fasciatus* n.sp., a new catshark (Chondrichthyes: Carcharhiniformes: Scyliorhinidae) from tropical Australia. Records of the Australian Museum 45(2): 147–169.

The genus *Atelomycterus* was proposed by Garman (1913) for *Scyllium marmoratum* Bennett, 1830, which has a wide range in the Indo-West Pacific from India and Pakistan to Malaya, Singapore, Indonesia, New Guinea, Thailand, Viet Nam, Philippines, southern China, and Taiwan (Fowler, 1941, Springer, 1979, Compagno, 1984, 1988). Whitley (1939) named a second species, *A. macleayi*, from Queensland, Western Australia and Northern Territory. *Atelomycterus macleayi* is readily separable from *A. marmoratus* (Bennett, 1830) by colouration and clasper morphology (Compagno, 1984, 1988).

McKay (1966) recorded *A. marmoratus* from Western Australia based on three specimens, but examination of his material in the Western Australian Museum (Perth) revealed two species: a hatchling *A. macleayi* and two specimens of a new species of *Atelomycterus* that differs from *A. macleayi* and *A. marmoratus* in colouration, morphometrics, clasper structure, vertebral counts, and smaller size (Compagno, 1984, 1988).

Recent offshore trawl surveys on the outer continental shelves and upper slopes of Australia (Gloerfelt-Tarp & Kailola, 1984; Davis & Ward, 1984; Sainsbury *et al.*, 1985; Gorman & Graham, 1985; Williams, 1987) produced a wealth of specimens of scyliorhinid catsharks along with many other sharks and bony fishes. Included in these collections is much additional material of the new *Atelomycterus*, which is described here as *A. fasciatus* new species.

Terminology and Abbreviations

The terminology for external structures, chondrocrania, vertebrae and dentition follows Compagno (1970, 1988). For vertebrae, an additional abbreviation PC is introduced for precaudal (monospondylous + diplospondylous precaudal) vertebral counts. The abbreviations and methods of measuring follow the FAO system of Compagno (1984), except that the measurement MOL (mouth length) was incorrectly shown in the diagram (Compagno, 1984: 12) as extending from the lower symphysis to the mouth corners; it should be from the *upper* symphysis to the mouth corners. Also, TL is used for total length and PCL for precaudal length (following general usage in ichthyology) instead of TOT and PRC. The abbreviations for measurements in this account include: TL (TOT) – total length; PCL (PRC) – precaudal length; PRN – prenarial length; POR – preoral length; POB – preorbital length; PSP – prespiracle length; PGI – pregill (prebranchial) length; HDL – head length; PP1 – prepectoral length; PP2 – prepelvic length; SVL – snout-vent length; PAL – preanal length; PD1 – pre-first dorsal length; PD2 – pre-second dorsal length; IDS – interdorsal space; DCS – dorsocaudal space; PPS – pectoral-pelvic space; PAS – preanal space; ACS – anal-caudal space; EYL – eye length; EYH – eye height; INO – interorbital width; NOW – nostril width; INW – internarial width; ANF – anterior nasal flap length; SPL – spiracle length; ESL – eye-spiracle length; MOL – mouth length; MOW – mouth width; ULA – upper labial furrow length; LLA – lower labial furrow length; GS1 – first gill opening height; GS2 – second gill opening height; GS3 – third gill opening height; GS4 – fourth gill opening height; GS5 – fifth gill opening height; HDH – head height; HDW – head width; TRH – trunk height; TRW – trunk width; CPH – caudal peduncle height; CPW – caudal peduncle width; GIR – girth; P1L – pectoral length; P1A – pectoral anterior margin; P1B – pectoral base; P1H – pectoral height; P1I – pectoral inner margin; P1P – pectoral posterior margin; P2L – pelvic length; P2A – pelvic anterior margin; P2B – pelvic base; P2H – pelvic height; P2I – pelvic inner margin; P2P – pelvic posterior margin; CLO – clasper outer length; CLI – clasper inner length; CLB – clasper base width; D1L – first dorsal length; D1A – first dorsal anterior margin; D1B – first dorsal base; D1H – first dorsal height; D1I – first dorsal inner margin; D1P – first dorsal posterior margin; D2L – second dorsal length; D2A – second dorsal anterior margin; D2B – second dorsal base; D2H – second dorsal height; D2I – second dorsal inner margin; D2P – second dorsal posterior margin; ANL – anal length; ANA – anal anterior margin; ANB – anal base; ANH – anal height; ANI – anal inner margin; ANP – anal posterior margin; CDM – dorsal caudal margin; CPV – preventral caudal margin; CPL+U – combined lower and upper postventral caudal margin; CST – subterminal caudal margin; CTR – terminal caudal margin; CTL – terminal caudal lobe; DAO – second dorsal-anal origin; DAI – second dorsal-anal insertion.

The criteria for assessing sexual maturity, and maturity stage, follow Compagno (1988). Stage 1 indicates embryos or fetuses, 2 immatures, 3 adolescents and 4 adults.

Comprehensive measurements were taken for the ten type specimens of *Atelomycterus fasciatus* and converted to proportions as percentages of total length (Table 1). Similar measurements and proportions were taken for three specimens of *A. macleayi* and nine *A. marmoratus* (Table 2) for comparison with the types of *A. fasciatus*. Selected morphometrics that suggested consistent differences between these two samples (PCL, POR, HDL, D1H, ANB, ANH, CLO, CLI, CLB) were then taken along with total length and weight for 62 additional specimens of *A. fasciatus*, for graphic and statistical comparison (Fig.14, Table 4) and analysis of differences between the three species.

Abbreviations and prefixes for field, accession and catalog numbers follow Leviton *et al.* (1986) and Compagno (1988) in part: BPBM – Bernice P. Bishop Museum, Honolulu, Hawaii; AMS – Australian Museum, Sydney, CSIRO CA and H – CSIRO Marine Laboratories, Hobart, Tasmania; CAS – California Academy of Sciences, San Francisco; LACM – Los Angeles County Museum of Natural History; LJVC – L.J.V. Compagno cataloged collection; NTM – Northern Territory Museum, Darwin; SU – Stanford University Division of Systematic Biology fish collection, now housed at CAS. USNM – United States National Museum of Natural History, Washington, D.C.; SO – CSIRO RV 'Soela' station number; WAM – Western Australian Museum, Perth. Abbreviations for statistics include: cv – coefficient of variation (100 x standard deviation/mean); n – number of specimens; sd – standard deviation.

All tables are listed in the Appendix.

Scyliorhinidae Gill, 1862

Atelomycterinae White, 1936

Comments. Compagno (1988) presented discussions and definitions of the subfamilies of Scyliorhinidae. The Atelomycterinae includes two genera: *Aulohalaelurus* Fowler, 1934, with *A. labiosus* (Waite, 1905) and *A. kanakorum* Seret, 1990, and *Atelomycterus* Garman, 1913, with *A. marmoratus* (Bennett, 1830), *A. macleayi* Whitley, 1939, and *A. fasciatus*.

Atelomycterus Garman, 1913

Atelomycterus Garman, 1913: 100. Type species *Scyllium marmoratum* Bennett, 1830, by monotypy.

Definition. Slender-bodied, narrow and short-headed cylindrical catsharks with thick, tough skin and well-calcified dermal denticles. Stomach not inflatable. Tail

moderately long, length from vent to lower caudal fin origin about four-fifths of snout-vent length. Snout short, rounded-parabolic or angular in dorsoventral view; ampullal pores not greatly enlarged on snout. Nostrils enlarged but with incurrent and excurrent apertures only slightly open to exterior; anterior nasal flaps very large, broad, triangular, nearly meeting each other at midline of snout and extending posteriorly to overlap mouth; nasoral grooves connecting mouth and nostrils, covered by anterior nasal flaps. Eyes dorsolateral on head, with narrow subocular ridges below eyes. Mouth angular or semiangular, teeth only slightly exposed; very long labial furrows on both jaws, uppers extending in front of upper symphysis. Branchial region very short, gill slits lateral on head. Well-differentiated rows of posterior teeth present along distal surface of mouth. Two dorsal fins present, equal sized or with second slightly larger than first; origin of first dorsal varying from over pelvic fin midbases to over their insertions; second dorsal fin origin over the first quarter of the anal fin base. Inner margins of pelvic fins not fused over claspers in adult males. Claspers with anterior tab on cover rhipidion; pseudosiphon greatly elongated. Anal fin small, not greatly elongated, smaller than pelvic and dorsal fins; anal origin far behind pelvic bases, insertion well anterior to lower caudal fin origin. Caudal fin short and broad, less than a fifth of total length in adults, without crests of enlarged denticles. Supraorbital crests present on cranium. Vertebral centra strongly calcified, with prominent, wedge-shaped, hollow intermedialia and large diagonal calcified lamellae. Total vertebral counts 149 to 183. Colour pattern of dark and light spots and dark saddles and bands present.

For a more detailed definition of this genus see Compagno (1988).

Comparative Material

Atelomycterus macleayi. AUSTRALIA: AMS I5269, 488 mm adult male, Port Darwin, NT. HOLOTYPE of *A. macleayi* Whitley, 1939; USNM 174070, 481 mm adult male, near Darwin, East Point Reef, NT; WAM P8811, 100 mm hatchling male, Cygnet Bay, King Sound, WA; NTM 50183, 390 mm female, near Darwin, East Point Reef, NT.

Atelomycterus marmoratus. NO DATA: LJVC-0325, 443 mm immature female. SINGAPORE: LACM Applegate uncatalogued, 491 mm adult female; SU 14182, 467 mm adult male; SU 40095, 395 mm immature female (semi-albino). PHILIPPINE ISLANDS: SU 13562, 615 mm adult male, Linapucan Island; SU 13563, 570 mm adult female, Sitankai, Sibutu Island; SU 13659, 477 mm adult male, Dumaguete, Negros Island; SU 13689, 472 mm immature female, Siasi Island; LACM 37431-1, 428 mm immature female, Pangasinan, near Bolinao. BPBM 29851, 614 mm adult female, Lombok, Batu Nampar fish market, Indonesia.

Key to the Species of *Atelomycterus*

1. Dorsal fins not angled rearwards, posterior margins sloping posteroventrally from fin apices. Dark brown spots and markings sparse, colour pattern dominated by brownish-grey saddles and bands on light background ..... *Atelomycterus fasciatus* n.sp.

—— Dorsal fins angled rearwards, posterior margins vertical or sloping anteroventrally from fin apices. Dark brown spots and markings dominating colour pattern 2

2. Colour pattern of brownish-grey saddles separated by light areas and outlined by numerous relatively small dark brown spots in adults; hatchlings have a simpler pattern of dusky saddles ..... *Atelomycterus macleayi* Whitley, 1939

—— Saddle markings obsolete, light grey and white spots outlined by large dark brown spots, bars and lines ..... *Atelomycterus marmoratus* (Bennett, 1830)

Atelomycterus fasciatus n.sp.

Banded sand catshark

Figs 1-4, 5A,B, 6-11

Atelomycterus marmoratus.–McKay, 1966, in part: 66, fig.1c,d (WAM P8629) [not fig.1a,b (WAM P8811) which is *A. macleayi*]

Atelomycterus sp.–Sainsbury *et al.*, 1985: 25 (illustration).–Compagno, 1988: 102-103, 393.

Atelomycterus (undescribed species).–Compagno, 1984: 292.–Sainsbury *et al.*, 1985: 24, illust.–Paxton *et al.*, 1989: 72.

Type material. HOLOTYPE, WAM P8629, 369 mm adult male, Onslow, WA (Fig.1).

PARATYPES, 9 (216-413 mm TL): WESTERN AUSTRALIA: CSIRO CA3289, SO2/82/57, 395 mm female, 16 Apr. 1982, 18°59'S 118°04'E, 100 m; WAM P23838, 251 mm immature male, 1973, 22°05'S 114°15'E; CSIRO H-1295-01, SO3/83/42, 400 mm adult male, 8 June 1983, 19°50'S 116°13'E, 68 m; CSIRO CA4518, SO3/83/44, 216 mm immature female, 9 June 1983, 20°23'S 116°04'E, 38 m; CSIRO CA4524, SO3/83/56, 318 mm immature female, 10 June 1983, 19°41'S 116°51'E, 66 m; CSIRO CA4523, SO3/83/61, 264 mm immature male, 11 June 1983, 20°22'S 117°22'E, 27 m; CSIRO H1297-01, SO3/83/96, 234 mm immature male, 16 June 1983, 20°00'S 117°52'E, 40 m; CSIRO H1294-01, SO3/83/111, 372 mm adult female; 17 June 1983, 19°59'S 117°51'E, 39 m; CSIRO H1296-01, SO6/86/26, 413 mm adult female, 12 Oct. 1986, 20°00'S 115°47'E, 66 m.

Non-type material. 69 (166-421 mm TL): WESTERN AUSTRALIA: CSIRO H1300-02, 366 mm adult female, CSIRO H1300-03, 364 mm early adult female, CSIRO H1300-04, 347 mm adolescent female, all 3 from SO1/83, 15 Feb. 1983, about 19°15'S 118°45'E; CSIRO H1300-01, 361 mm adult male, SO1/83/01, 15 Feb. 1983, 20°02'S 117°48'E, 40 m; CSIRO H1300-05, 302 mm early adolescent male, SO1/83/06, 15 Feb. 1983, 20°22'S 116°39'E, 27 m; CSIRO CA4515, 353 mm adolescent female, CSIRO CA4514, 389 mm late adolescent female, both from SO2/83/60, 2 Apr. 1983, 19°32'S 118°45'E, 35 m; CSIRO CA4513, 254 mm immature female, SO3/83/06, 2 June 1983, 19°50'S 117°34'E, 52 m; CSIRO H1295-02, 402 mm adult male, CSIRO H1295-03, 392 mm early adult female, both from SO3/83/42, 8 June 1983, 19°50'S 116°13'E, 68 m; CSIRO H1306-01, 378 mm adult female, SO3/83/77, 15 June 1983, 20°00'S 117°51'E, 41 m; CSIRO H1308-01, 379 mm adult female, SO3/83/88, 16 June 1983, 19°59'S 117°50'E, 42 m; CSIRO H1297-02, 352 mm adult (gravid) female, CSIRO H1297-03, 353 mm adult male, both from SO3/83/96, 16 June 1983, 20°00'S 117°52'E, 40 m; CSIRO H1303-01, 329 mm adult male, SO3/83/97, 16 June 1983, 20°00'S 117°51'E, 39 m; CSIRO H1304-01, 245 mm immature female, CSIRO H1304-02, 383 mm early adult female, both from SO3/83/99, 17 June 1983, 19°59'S 117°51'E, 40 m; CSIRO H1305-01, 362 mm adult male, SO3/83/101, 27 June 1983, 20°00'S 117°52'E, 41 m; CSIRO H1307-01, 310 mm adolescent male, CSIRO H1307-02, 370 mm adult female, both from SO3/83/110, 17 June 1983, 19°59'S 117°52'E, 40 m; CSIRO H1294-02, 286 mm immature female, CSIRO H1299-10, 372 mm adult (gravid) female, both from SO3/83/111, 17 June 1983, 19°59'S 117°51'E, 39 m; CSIRO CA4522, 255 mm immature male, SO4/82/22, 11 Aug. 1982, 19°50'S 118°02'E, 44 m; CSIRO CA4520, 311 mm early adolescent male, CSIRO CA2451, 246 mm immature male, both from SO4/83/28, 6 Aug. 1983, 20°03'S 117°51'E, 35 m; CSIRO CA4519, 253 mm immature female, SO5/82/46, 10 Feb. 1983, 19°02'S 117°58'E, 104 m; CSIRO H1301-01, 387 mm adult male, SO5/82/64, 5 Oct. 1982, 19°30'S 117°48'E, 62 m; CSIRO H1299-08, 401 mm adult male, CSIRO H1299-11, 420 mm adult female, CSIRO H1302-01, 421 mm adult female, CSIRO H1302-02, 372 mm adolescent female, CSIRO H1302-03, 398 mm adult female, CSIRO H1302-04, 384 mm adult male, all 6 from SO6/82/101, 28 Nov. 1982, 20°10'S 117°20'E, 40 m; CSIRO H1095-01, 335 mm immature female, CSIRO H1095-02, 264 mm immature male, both from SO7/87/20, 3 Oct. 1987, 20°14'S 116°48'E, 41 m; CSIRO CA1290, 338 mm female, SO7/80/19, 7 Nov. 1980, 18°37'S 119°24'E, 120 m; CSIRO CA1293, 357 mm adult male, SO4/80/51, 6 June 1980, 18°37'S 119°20'E, 122 m; CSIRO CA1294, 364 mm female, SO7/80/6, 4 Nov. 1980, 20°09'S 116°07'E, 76 m; CSIRO CA1295, 270 mm female, SO4/80/56, 7 June 1980, 19°33'S 119°31'E, 34 m; CSIRO H1223-01, 271 mm immature female, Feb. 1988, Albatross Bay (skeletonised); CSIRO H1298-01, 298 mm immature male, CSIRO H1298-02, 379 mm adult (early) female, CSIRO H1298-03, 186 mm immature female, CSIRO H1298-04, 378 mm adult female, CSIRO H1298-05, 381 mm adult

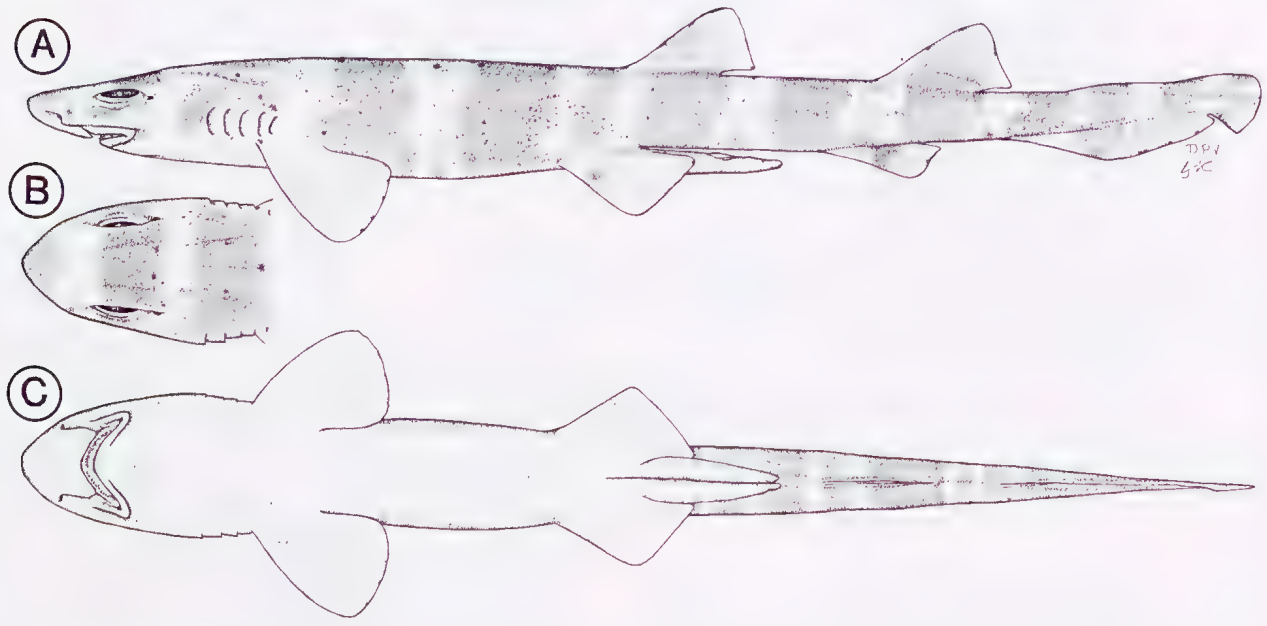

Fig.1. *Atelomycterus fasciatus* n.sp., holotype, WAM P8629, 369 mm adult male. A, lateral view; B, dorsal view of head; C, ventral view. (The majority of specimens have more numerous spots than the holotype and have incomplete saddle markings posterior to the pelvic fins rather than encircling bands.) Illustration by D. Voorfelt and L.J.V. Compagno.

(early) female, CSIRO H1298-06, 395 mm adult male, CSIRO H1298-07, 368 mm adult male, CSIRO H1298-08, 180 mm immature male, CSIRO H1298-09, 400 mm adult male, CSIRO H1298-10, 240 mm immature female, CSIRO H1298-11, 373 mm adult male, CSIRO H1298-12, 166 mm immature female, CSIRO H1299-09, 405 mm adult (gravid) female, CSIRO H1299-13, 272 mm immature female, all 14 from 'Coral Reeftel', 15 May 1983, North West Shelf; CSIRO CA4517, 359 mm adult male, CSIRO CA4516, 386 mm adult male, both dated 19 Sept. 1982, no further data; CSIRO H1299-01, 370 mm adult male, CSIRO H1299-02, 393 mm adult female, CSIRO H1299-03, 314 mm early adolescent female, CSIRO H1299-04, 380 mm adult female, CSIRO H1299-05, 413 mm adult female, CSIRO H1299-06, 252 mm immature female, CSIRO H1299-07, 241 mm immature female, CSIRO H1299-12, 394 mm adult female, CSIRO H1299-14, 400 mm adult female, CSIRO H1349-01, 180 mm immature male, all 10 from North West Shelf but with no further data. NORTHERN TERRITORY: AMS I.21842-001, 375 mm female, from SO7/80/43P, 16 Nov. 1980, Arafura Sea, 10°37'S 133°47'E, 60 m. QUEENSLAND: AMS I.15557-003, 270 mm adult male, 1964, 16°38'S 140°02'E, 32 m; CSIRO H1118-01, 300 mm immature male, 4 Nov. 1987, Torres Strait, 10°31'S 140°48'E, 43 m.

Diagnosis. *Atelomycterus* with a relatively long snout, preoral length 4.4-5.6% TL. Head length 18.4-21.3% TL, precaudal length 77.8-86.1% TL. Dorsal fins broadly triangular, not semifalcate, with posterior margins sloping posteroventrally from fin apices. Adult claspers elongated but broad, thick, tapering from base to tip, clasper outer length 9.3-11.2% TL, clasper base width 12.7-17.4% of clasper outer length. Clasper glans slightly more than half length of clasper; an enlarged tab on cover rhipidion; cover rhipidion large; rhipidion moderately large, relatively low, but mostly concealed by cover rhipidion and exorhipidion; exorhipidion large and overlapping base of cover rhipidion; pseudosiphon over half length of cover rhipidion; pseudopera large; clasper tip narrow, bluntly pointed. Clasper shaft stout, hourglass-shaped; dorsal and ventral terminal cartilages long; end-style long; accessory dorsal terminal (TD2) not greatly elongated. Anal fin smaller than in other species, height 1.6-3.3% TL and base 7.2-7.3% TL. Total vertebral counts 149-161 (N = 9), precaudal counts 100-110 (N = 18). Colour pattern of broad brownish saddles and transverse bands on tan background, with scattered small dark brown and sometimes small white spots; brownish saddles on abdomen extend ventrally to, or slightly below, line between pectoral and pelvic fin bases, brownish bands occasionally encircle precaudal tail. Size small, adult females to 451 mm TL and 258 g weight.

Etymology. Latin *fasciatus*, banded, in reference to its colour pattern.

Description. Proportions as percentages of total length for holotype and paratypes (9) are presented in Table 1.

Head short, length about equal (0.9-1.1) to pectoral-pelvic space. Head narrow and depressed, roughly trapezodial in cross-section at eyes. Outline of head in lateral view convex dorsally, with slight concavity in front of eyes; in dorsoventral view head with narrow parabolic outline anterior to gill openings. Preoral snout short, 0.7-0.9 times mouth width, broadly rounded in dorsoventral view, not indented anterior to nostrils; snout bulbous and bluntly pointed in lateral view, convex above and below.

External eye openings with prominent anterior and posterior eye notches; eyes small and spindle-shaped, eye length 5.1-7.0 in head length and 2.0-3.8 times eye height. Eyes dorsolateral on head, with lower edges well

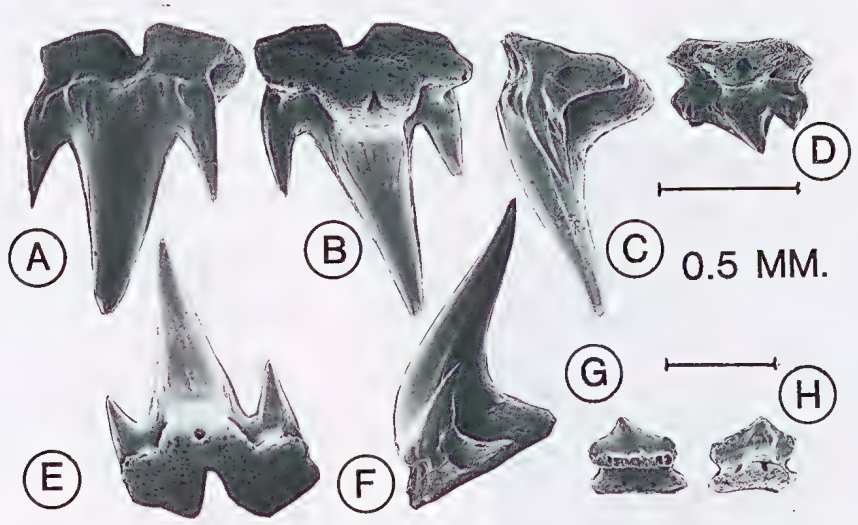

Fig.2. *Atelomycterus fasciatus*, scanning electron micrographs of representative teeth from CSIRO H1296.01, 413 mm adult female. A-D, upper teeth, enlarged to about 1.2 times the size of the lower teeth; E-G, lower teeth. A-C, upper anterolateral teeth from near symphysis in A, labial, B, lingual and C, mesodistal views; D, posterior tooth in lingual view; E-F, lower anterolateral teeth from near symphysis in E, lingual and F, mesodistal views; G-H, posterior teeth in G, labial and H, lingual views. Scale bars = 0.5 mm, differing for upper and lower teeth. Photos by A.J. Rees.

medial to horizontal head rim in dorsal view, subocular ridges strong but narrow. Nictitating lower eyelids of rudimentary type, with shallow, scaled subocular pouches and secondary lower eyelids free from upper eyelids.

Spiracles small, length 3.8-8.5 in eye length, 0.1-0.3 eye lengths behind and below posterior eye notch. First four gill openings usually higher than fifth, height of fifth 0.5-1.0 of third; height of third 7.1-15.6 in head and 0.4-0.8 of eye length. Gill openings straight, undulated, or slightly concave, gill filaments not visible from outside. Upper ends of gill openings about opposite lower edges of eyes, gill openings not elevated on dorsolateral surface of head. Gill-raker papillae absent from gill arches.

Nostrils with very small incurrent apertures lacking posterolateral keels, broadly angular nasal flaps with narrowly rounded tips, very small mesonarial flaps well lateral on anterior nasal flaps, large excurrent apertures, no posterior nasal flaps. Nostrils reaching mouth, with anterior nasal flaps partly covering upper symphysis. Anterior nasal flaps very large, meeting at midlength of mouth, covering excurrent apertures. Nostril width 0.8-1.1 in internarial space, 1.1-2.0 in eye length, and 0.6-1.6 in third gill opening height.

Mouth broadly angular, small, short, mouth width 2.7-3.4 in head length; mouth length 2.1-3.1 in mouth width. Lower symphysis nearly reaching upper symphysis, teeth exposed in ventral view. Tongue moderate-sized, flat and rounded, filling most of floor of mouth. Maxillary valve narrow, not highly papillose. No large buccal papillae in mouth, palate and floor of mouth covered with buccopharyngeal denticles, except for just in front of tongue. Upper labial furrows long, reaching upper symphysis, lower furrows 0.8-1.0 times upper furrows. Labial cartilages large.

Teeth in 56-73/50-59 rows; 2-5/3-8 series functional, with more series functional in adults than young and in posterior tooth rows than anterolaterals. Lateroposterior teeth not arranged in diagonal files, no toothless spaces at symphysis. Teeth not strongly differentiated in upper and lower jaws but with tooth row groups along jaws, including weakly defined medials (M), anterolaterals (AL) and posteriors (P) in both jaws. Tooth formula (N = 7) is:

$$\text{Left}\quad \frac{\text{P9-13 AL18-23 M3 AL19-21 P7-14}}{\text{P9-11 AL14-16 M3 AL14-18 P8-13}}\quad \text{Right}$$

or

$$\frac{\text{28-35 3 27-35}}{\text{23-27 3 22-30}}$$

Sexual heterodonty apparently absent, teeth not enlarged or particularly modified in adult males. Upper anterolateral teeth (Fig.2A-C) smaller, with slightly broader crowns and longer cusplets than lowers (Fig.2E,F), with well-developed transverse ridges (absent in lower anteroposteriors). Weakly differentiated medials are smaller than anterolaterals, which have strong erect to semioblique cusps, usually 1 strong cusplet on either side, strong basal ledges and grooves, transverse ridges confined to the basal ledges where present, and low, thick, flat roots. Several rows of strikingly smaller posteriors with low weak cusps are present in both jaws, uppers (Fig.2D) differing from lowers (Fig.2G,H) in having stronger cusplets; posterior teeth not comblike, with cusp not strongly shifted posteriorly on crown foot. Gradient monognathic heterodonty well developed in anterolateral teeth; anteroposteriors distally smaller, with thicker and more oblique cusps and lower cusplets. Sample teeth examined either with no transverse groove (anaulacorhizous in most distal teeth) or a partially developed labial groove (hemiaulacorhizous) with prominent centrolingual foramen on linguobasal attachment surface of roots and disto- and mesolingual foramina on sides of teeth. Tooth histological type (histotype) orthodont as seen

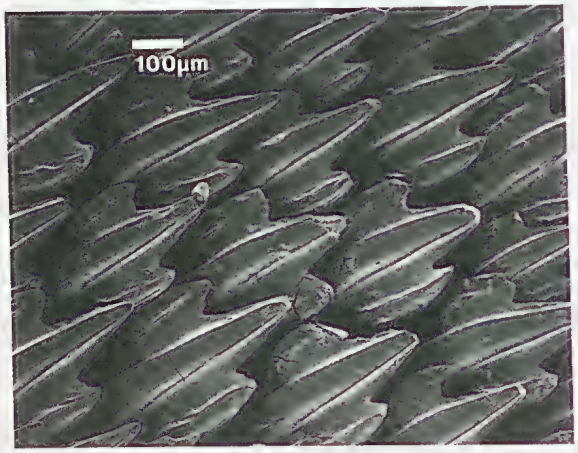

Fig.3. *Atelomycterus fasciatus*, scanning electron micrograph of lateral trunk denticles in three-quarter anteriorlateral view, from CSIRO H1296.01, 413 mm adult female. Photo by A.J. Rees.

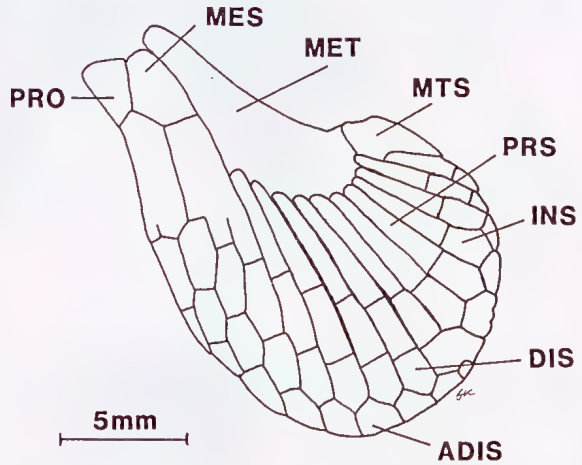

Fig.4. *Atelomycterus fasciatus*, pectoral fin skeleton, CSIRO H1223.01, 271 mm immature male. Abbreviations: ADIS – accessory distal radial segments; DIS – distal radial segments; INS – intermediate radial segments; MES – mesopterygium; MET – metapterygium; MTS – metapterygial segment (axis); PRO – propterygium; PRS – proximal radial segments. Illustration by L.J.V. Compagno.

by transmitted light through teeth in water, with a pulp cavity.

Body fairly slender, trunk virtually circular in section at first dorsal base, length of trunk from fifth gill openings to vent 0.9-1.3 times head length. No predorsal, interdorsal or postdorsal ridges on midline of back, no postanal ridge between anal fin base and lower caudal fin origin; lateral ridges absent from body. Caudal peduncle short, fairly thick, vertically oval or circular in section, without lateral keels, caudal peduncle height 1.0-1.3 of its width at second dorsal fin insertion, 1.5-2.6 in dorsal-caudal space.

Lateral trunk denticles below first dorsal fin with flat, smooth, elongated teardrop-shaped crowns about 1.5 times as long as wide (Fig.3). Crown with pair of strong medial ridges extending entire length of crown onto long, strong, narrow medial cusp; pair of low but prominent lateral ridges extending onto short, obtuse, relatively broad lateral cusps. Denticle crowns closely spaced and well-imbricated. Denticles varying little with growth; young have lateral trunk denticles with slightly narrower crowns and narrower medial cusps than adults.

Pectoral fins broad and rounded-triangular, not falcate, with broadly convex anterior margins, narrowly rounded apices, broadly rounded posterior margins, free rear tips, inner margins and narrow bases. Pectoral fin anterior margin 1.0-1.2 times pectoral fin length. Pectoral fins slightly less than twice area of first dorsal fin. Origins of pectoral fins under interspace between third and fourth gill openings. Apex of pectoral fin slightly anterior to its free rear tip when fin is elevated and appressed to body.

Pectoral fin skeleton (Fig.4) aplesodic, with longest radials extending about 0.4 of pectoral fin anterior margin length into fin. Radials mostly divided into 3 (propterygial and posteriormost metapterygial radials) or 4 (mesopterygial and anterior 5 metapterygial radials) segments, longest distal segment 0.6 times length of its proximal segment. Pectoral skeleton tribasal, propterygium with single radial; mesopterygium with 4 radials, proximal segment of anteriormost fused anteriorly to propterygial radial, proximal segments of posterior 3 fused together; metapterygium with 10

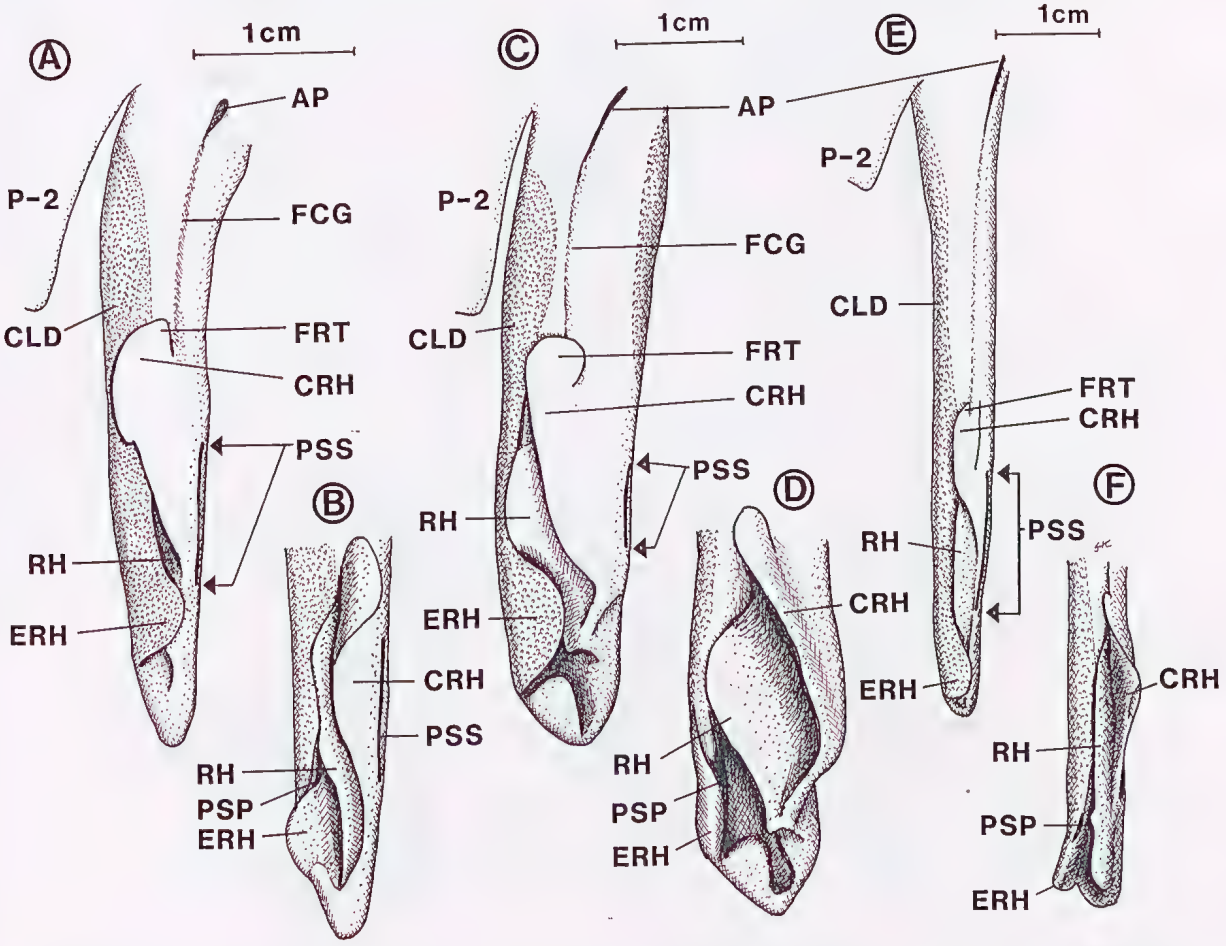

Fig.5. Claspers of *Atelomycterus* species, all from adult males. A-B, *Atelomycterus fasciatus*, WAM P8629, 369 mm holotype; C-D, *Atelomycterus macleayi*, USNM 174070, 481 mm; E-F, *Atelomycterus marmoratus*, SU 14182, 467 mm. A,C,E – glans not dilated; B,D,F – glans spread. Abbreviations: AP – apopyle; CLD – clasper denticles; CRH – cover rhipidion; ERH – exorhipidion; FCG – fused clasper groove; FRT – free tab on cover rhipidion; P-2 – pelvic fin; PSP – pseudopera; PSS – pseudosiphon; RH – rhipidion. Illustration by L.J.V. Compagno.

unfused radials on basal segment and 1 on metapterygial axis; total radial count 16. Propterygium short and wedge-shaped, broad basally and distally narrow. Mesopterygium and metapterygium not separated by a fenestra; mesopterygium short, irregularly pentagonal, only slightly elongated mesodistally. Metapterygial basal segment triangular, elongated diagonal to axes of its radials. Metapterygial axis short, without a segment, with length about 0.4 of metapterygial basal segment.

Pelvic fins broadly triangular; pelvic anterior margins 0.6-0.8 of pectoral-fin anterior margins; pelvic area 2-3 times anal fin area. Pelvic-fin anterior margins nearly straight, apices narrowly rounded, posterior margins convex or nearly straight, free rear tips narrowly rounded and not attenuated, inner margins straight or slightly convex and not fused together over claspers of adult males.

Claspers (Fig.5A,B) relatively long and basally stout, convex and strongly tapering on lateral edge, with a slightly undulated, blunt-tipped clasper glans. Claspers of adult males extending well behind pelvic-fin free rear tips by distance about 1.7 of pelvic-fin inner margin, but falling in front of anal fin origin by about 0.4 of anal fin base. Most of clasper except dorsomedial and posteromedial surface of glans (including rhipidion) and a lateral strip adjacent to clasper groove covered with small clasper denticles with anteriorly directed cusps. Exorhipidion strongly differentiated, originating opposite last third of cover rhipidion, with a blunt apex and long base but without specialised clasper hooks. Pseudopera present below anterior end of exorhipidion and about opposite posterior end of cover rhipidion, relatively broad and shallow. No envelope present anterior to hypopyle. Rhipidion present and very large, extending over most of length of clasper glans formed as a flat, convex-edged blade with posterior end below apex of exorhipidion. Cover rhipidion very large, formed as distally tapering wedge with large, lobate anterior tab, extending from apopyle to apex of exorhipidion. Pseudosiphon very long, narrow, slitlike, extending opposite most of base of cover rhipidion.

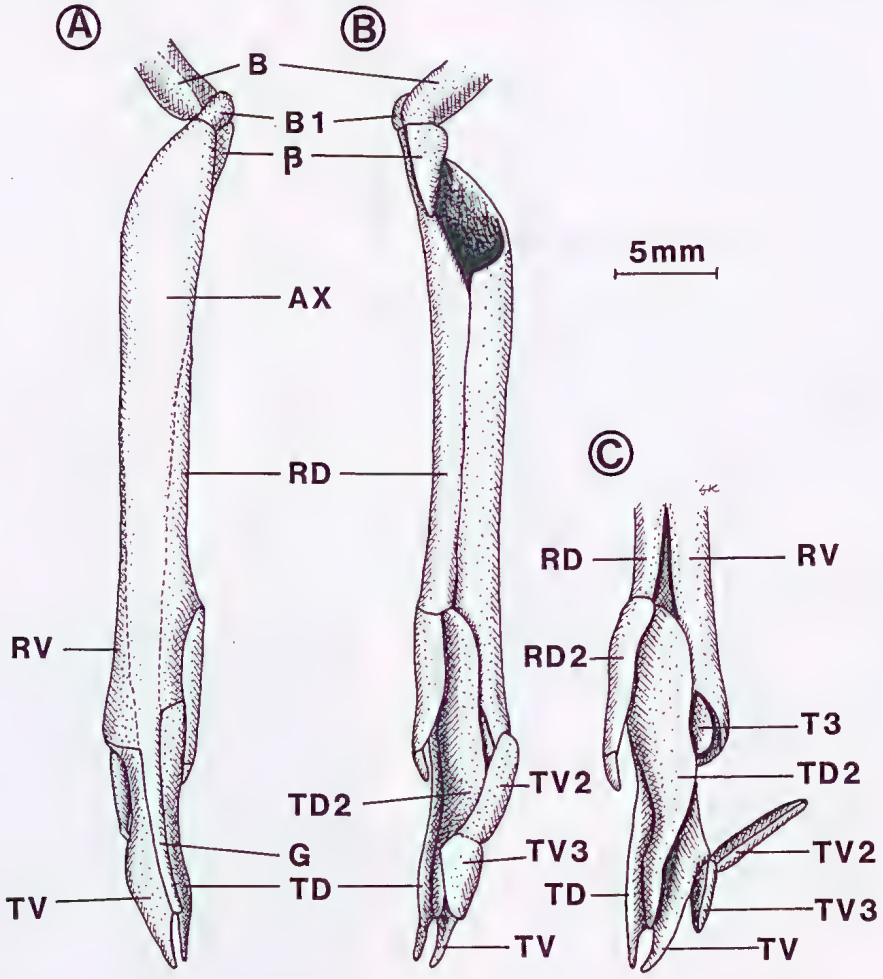

Fig.6. *Atelomycterus fasciatus*, clasper skeleton, CSIRO CA4517, 359 mm adult male, right side. A, ventral view; B, dorsal view, terminal cartilages not dilated; C, dorsal view of glans, terminal cartilages spread. Abbreviations: AX – axial cartilage; ß – beta cartilage; B – basipterygium; B1 – intermediate segment; G – end-style; RD – dorsal marginal cartilage; RD2 – accessory dorsal marginal cartilage; RV – ventral marginal cartilage; T3 – accessory terminal cartilage; TD – dorsal terminal cartilage; TD2 – dorsal terminal 2 cartilage; TV – ventral terminal cartilage; TV2 – ventral terminal 2 cartilage; TV3 – ventral terminal 3 cartilage. Illustration by L.J.V. Compagno.

Apopyle and hypopyle connected by long clasper groove, with its dorsal margins usually fused over clasper canal (open in one adult male examined). Clasper siphons moderately long and narrow, extending anterior to level of pectoral-fin free rear tips.

Clasper skeleton with all elements present (Fig.6). Axial cartilage or appendix-stem connected proximally by single very short intermediate segment (B1) and long, posteriorly tapering, wedge-shaped dorsal beta cartilage (ß) to pelvic basipterygium. Clasper shaft, formed from axial cartilage and tightly rolled dorsal and ventral marginal cartilages slender, tapering, then expanding posteriorly in elongated hourglass shape. Clasper glans skeleton with large, narrow, curved, pick-shaped dorsal terminal and more distally expanded, spear-shaped ventral terminal, articulating with and separated along their proximomesial three-fourths from narrow, cylindrical end-style (terminal extension of axial cartilage); short free posterior ends of terminal cartilages separated by a narrow gap, nearly straight. Accessory dorsal marginal cartilage (RD2) long, wedge-shaped, distally tapering, with separate short distal segment (RD3?) that supports cover rhipidion. Dorsal terminal 2 cartilage (TD2) large, elongated, bladelike, distally tapering, extending inside rhipidion along almost entire clasper glans from dorsal marginal to end-style tip. Ventral terminal 2 and 3 cartilages (TV2 and TV3) of exorhipidion include posteriorly tapering, wedge-shaped TV3 articulating anteriorly with lateral projection of TV, and elongated, rectangular TV2 articulating with anterolateral end of TV3 and extending anteriorly to partly cover distal end of ventral marginal. Short, broad accessory terminal cartilage (T3) present under anterior third of TD2 cartilage, partially sheathed by terminal extension of ventral marginal and well anterior to TV3-TV articulation.

First dorsal fin high, apically narrow and not falcate, with nearly straight or undulated anterior margin, narrowly rounded apex, nearly straight posterior margin, angular free rear tip, straight inner margin. First dorsal-fin origin over last third of pelvic-fin bases, midpoint of base well anterior to pelvic-fin free rear tips, insertion closer to pelvic-fin insertions than anal-fin origin, free rear tip 2-3 times length of inner margin anterior to anal-fin origin. Posterior margin slanting posteroventrally from fin apex, insertion varying from slightly in front to slightly behind dorsal-fin apex. First dorsal-fin base 1.4-2.1 in interdorsal space, 1.8-2.8 in dorsal caudal-fin margin; first dorsal-fin height 1.2-1.7 in first dorsal-fin base; first dorsal-fin inner margin 1.3-2.1 in first dorsal-fin height, 1.9-3.7 in first dorsal-fin base.

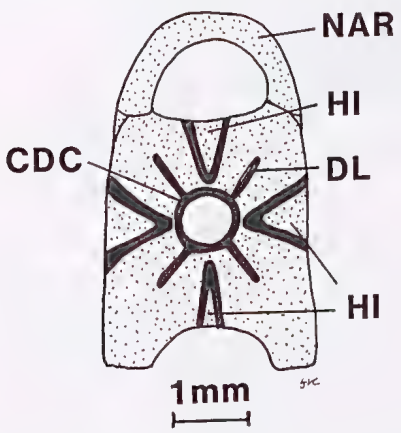

Fig.7. *Atelomycterus fasciatus*, vertebral calcification pattern, CSIRO H1223-01, 271 mm immature male. Abbreviations: CDC – calcified double cone; DL – diagonal calcified lamella; HI – hollow intermedialia; NAR – neural arch. Illustration by L.J.V. Compagno.

Second dorsal fin high, apically narrow, not falcate, subequal to first dorsal-fin area, second dorsal-fin height 0.8-1.1 of first dorsal-fin height, base 1.0-1.3 of first dorsal-fin base. Second dorsal fin with slightly convex anterior margin, narrowly rounded apex, nearly straight posterior margin, bluntly pointed free rear tip, and concave or straight inner margin. Second dorsal-fin origin opposite or slightly in front of anal-fin midbase, insertion well behind anal-fin free rear tip, and free rear tip in front of upper caudal-fin origin by 1-2 times its inner margin. Posterior margin slanting posteroventrally from apex, insertion below or slightly in front of dorsal apex. Second dorsal-fin base 0.6-0.9 in dorsocaudal space, second dorsal-fin height 1.5-2.0 in second dorsal-fin base, second dorsal-fin inner margin 1.5-2.2 in second dorsal-fin height and 2.6-3.8 in second dorsal-fin base.

Anal fin low, apically broad, not falcate, much smaller than second dorsal fin, anal-fin height 0.5-0.6 in second dorsal-fin height and base 0.7-1.0 times second dorsal-fin base. Anal-fin anterior margin slightly concave, nearly straight, or convex, apex broadly rounded, posterior margin slightly undulated, free rear tip bluntly pointed, and inner margin nearly straight. Anal-fin base without preanal ridges, anal-fin origin about 2.0-2.5 times anal-fin base length behind pelvic-fin insertions, free rear tip about 2.5-5.0 times anal-fin inner margin length anterior to lower caudal-fin origin. Anal-fin posterior margin slanting posterodorsally, anal-fin insertion posterior to apex. Anal-fin base 0.9-1.8 in anal-caudal space, anal-fin height 2.4-3.3 in anal-fin base, anal-fin inner margin 1.2-1.7 in anal-fin height and 3.1-4.7 in anal-fin base.

Caudal fin narrow and asymmetrical, with large terminal lobe and ventral lobe not developed. Caudal fin short, dorsal margin 4.3-5.1 in precaudal length. Preventral caudal-fin margin 1.8-2.5 in dorsal caudal-fin margin, terminal lobe 3.2-4.4 in dorsal caudal-fin margin, subterminal margin 1.1-1.8 in terminal margin. Dorsal caudal-fin margin without lateral undulations but proximally and distally convex with shallow concavity between the convexities. Preventral caudal-fin margin basally concave and apically straight, tip of ventral caudal fin lobe bluntly rounded. Postventral margin not differentiated into upper and lower parts, margin straight to convex. Subterminal notch a narrow, deep slot, subterminal margin straight to concave and terminal

margin convex and sometimes notched, lobe formed by these margins angular, tip of tail broadly rounded.

Vertebral counts, ratios and statistics given in Table 3. Transition between MP and DP centra about 4-8 centra behind front of pelvic girdle. Last few MP centra before MP-DP transition hardly enlarged, not forming 'stutter zone' of alternating long and short centra.

Vertebral calcification pattern (Fig.7) as in other atelomycterines (Compagno, 1988), with well-calcified hollow intermedialia, long diagonal calcified lamellae, and a well-calcified double cone.

Intestinal valve of conicospiral type, with 11-13 turns. Of 18 specimens counted 2 had 11, 10 had 12, 6 had 13 turns (mean = 12.2, sd = 0.6, cv = 5.3).

Chondrocranium (Fig.8) with short rostral cartilages, these slender, cylindrical, not hypercalcified. In one specimen examined these were free at their distal tips and did not form a discrete rostral node. Medial rostral cartilage approximately 27% of NBL, distance between bases of lateral rostral cartilages 1.8 in medial rostral cartilage. Medial rostral with distal spearlike expanded tip and ventral low prominence; lateral rostrals evenly tapering to their narrow tips. Nasal capsules large, high, transversely oval, and slightly wider than long, width across them 71% of NBL, length of capsule 1.1 in its width. Anterior margins of nasal capsules broadly convex. Nasal apertures nearly vertical, on anterolateral faces of capsules, separated from large nasal fontanelles by a broad channel. Ectethmoid chambers inside nasal cavities, at posterior edges of nasal fontanelles and not visible

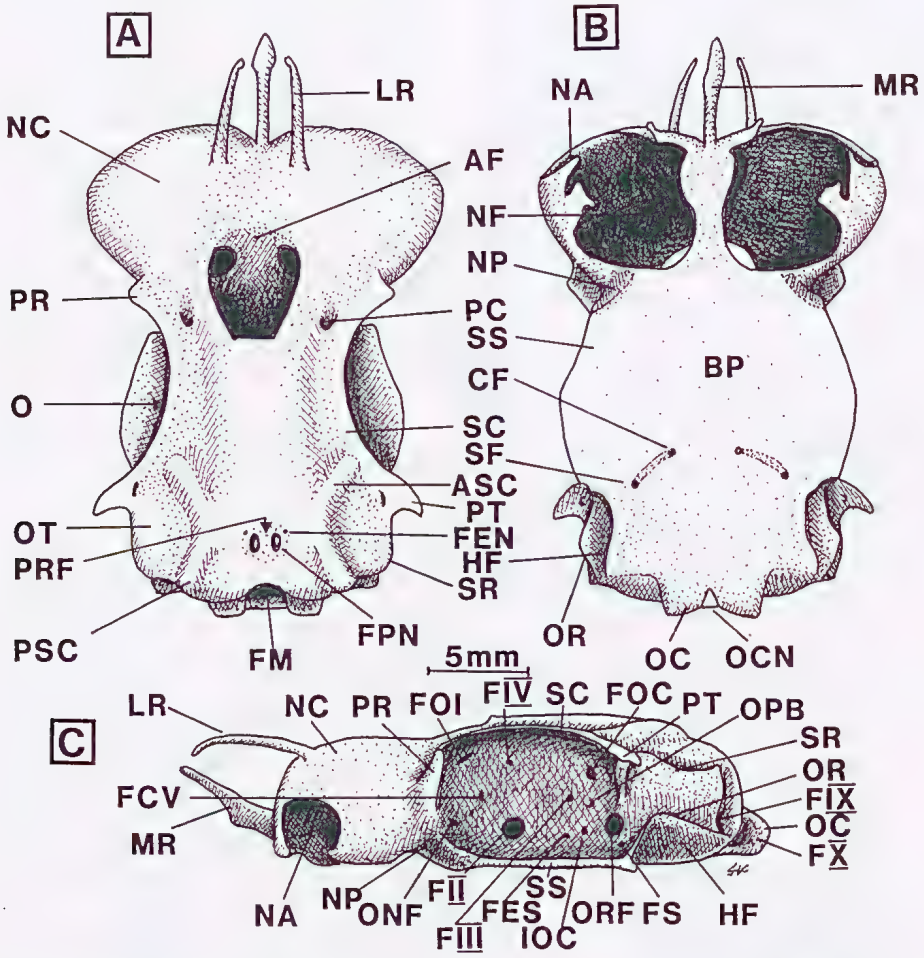

Fig.8. *Atelomycterus fasciatus*, chondrocranium, CSIRO H1223-01, 271 mm immature male. A, dorsal; B, ventral; C, lateral views. Abbreviations: AF – anterior fontanelle; ASC – anterior semicircular canal; BP – basal plate; CF – internal carotid foramen; FCV – foramen for anterior cerebral vein; FEN – endolymphatic foramen; FES – foramen for efferent spiracular artery; FM – foramen magnum; FOC – foramen for superficial opthalmic nerve; FOE and FOI – external and orbital foramina of preorbital canal; FPN – perilymphatic foramen; FII – optic nerve foramen; FIII – oculomotor nerve foramen; FIV – trochlear nerve foramen; FIX – glossopharyngeal nerve foramen; FX – vagus nerve foramen; HF – hyomandibular facet; IOC – interorbital canal; LR – lateral rostral cartilage; MR – medial rostral cartilage; NA – nasal aperture; NF – nasal fontanelle; NC – nasal capsule; NP – orbital notch; O – orbit; OPB – optic pedicel base; OC – occipital condyle; OCN – occipital centrum; ONF – orbitonasal foramen; OR – opisthotic ridge; ORF – orbital fissure; OT – otic capsule; PR – preorbital process; PRF – parietal fossa; PSC – posterior semicircular canal; PT – postorbital process; SC – supraorbital crest; SF – stapedial foramen; SR – sphenopterotic ridge; SS – suborbital shelf. Illustration by L.J.V. Compagno.

ventrally. Subnasal plate in form of short irregular medial extensions of lateral capsule wall, lateral extensions of narrow, high internasal septum bordering wide nasal fontanelles. Anterior fontanelle horizontally oval but with posterior edge transverse, width about 1.2 times in its length and about 20% of NBL. Dorsal lip of fontanelle slightly flared, without epiphysial foramen. Cranial roof flat between orbits, slightly elevated above supraorbital crests but not greatly arched or domelike. Parietal fossa shallow. Orbital notches relatively deep. Basal plate flat from orbital notches to occipital centrum, without keels. Internal carotid foramina slightly further from each other than from stapedial foramina. Edge of supraorbital crests arcuate in dorsal view, with short, prominent bluntly triangular preorbital processes and retroflexed, posteriorly hooked postorbital processes with basal foramina. Width across preorbital processes 59% of NBL, width across postorbital processes 71% of NBL, least width across supraorbital crests 1.8 in width across postorbital processes. Orbits horizontally subrectangular in lateral view, with contents indicated in Figure 8C. A weak ledge between suborbital shelves and nasal capsules. Suborbital shelves arcuate-angular in shape, extending well lateral to supraorbital crests in dorsal view. Width across suborbital shelves 63% of NBL. Otic capsules not greatly expanded or inflated, lengths about 27% of NBL, and greatest width across them 59% of NBL. Sphenopterotic ridges broadly arcuate in dorsal view, with slight pterotic horn in lateral view. Opisthotic ridges high, extending laterally to edges of sphenopterotic ridges. Hyomandibular facets very large, wedge-shaped, extending across entire length of otic capsules but not exserted posteriorly. Occipital condyles broad and prominently exserted from occiput, with a single occipital centrum between them.

Colour. In alcohol, colour light brownish grey above, lighter below on head, trunk, precaudal tail and fins, bands and saddles darker brownish grey. Broad dark

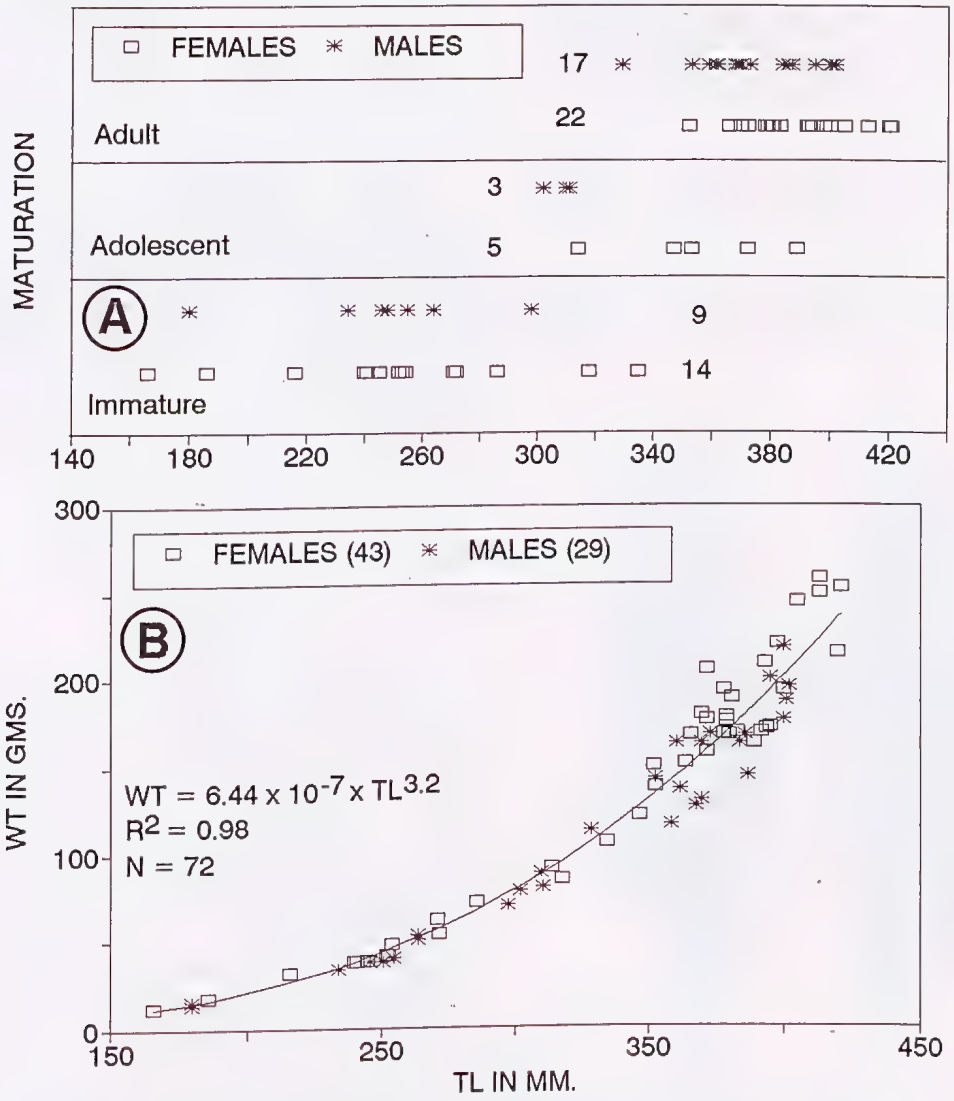

Fig.9. *Atelomycterus fasciatus* size plots. Females indicated by hollow squares, males by hollow diamonds. A, scatterplots of total lengths of immature, adolescent and adult specimens in the sample, separated by sex; B, length-weight plot of 72 individuals. Line indicates exponential regression curve combining both sexes, $WT = 6.44 \times 10^{-7} \times TL^{3.26}$, $R^2 = 0.98$.

brownish grey saddle-marks on snout tip, head above eyes, over and just in front of gills, over pectoral-fin inner margins, over abdomen just anterior to pelvic-fin bases, occasionally changing to encircling bands over pelvic-fin inner margins, between dorsal-fin bases, under second dorsal-fin base, at origins of caudal fins, continuing as 2 bands on caudal-fin web and 1 on caudal-fin terminal lobe. Secondary narrow dark bands variably developed over pectoral-fin bases, between broad bands on abdomen, over pelvic-fin bases, and between broad bands under first dorsal-fin free rear tip, under second dorsal-fin origin, below second dorsal-fin inner margin, and between bands on caudal fin; secondary bands usually lighter than primary dark bands. Small dark brown spots size of eye pupil or greater variably developed, scattered on head, body, dorsal-fin surfaces and precaudal tail. No prominent white tips or edges to fins. Small white spots either absent or variably developed, when present few to numerous, size of eye pupil or larger, and scattered over dorsal surface and sides of head, body, tail and dorsal surface of pectoral and pelvic fins, between and inside dark saddle marks and most other dark areas.

Size. Female *Atelomycterus fasciatus* probably mature at a greater size and attain a larger maximum size than males. A size-frequency scattergram comparing juveniles, adolescents and adults of both sexes of *A. fasciatus* is presented as Figure 9A. Nine immature males are 180 to 298 mm long, while three adolescent males are 302 to 311 mm long, and 17 adult males are 329 to 402 mm long (mean for adults 376 mm TL, sd = 19.9, cv = 5.3). Fourteen immature females are 166 to 335 mm long, while five adolescent females are 314 to 389 mm long and 22 adult females (including 3 with egg cases) are 352 to 451 mm long (mean for adults 388.1 mm TL, sd = 18.0, cv = 4.6). There is considerable overlap between juvenile and adolescent females, and between adolescent and adult males in the sample.

Average weight of adult males in our sample was about 82% of that of adult females, with considerable overlap between large males and small females. Adult males weighed 113 to 218 g (mean = 159.2, sd = 29.4, cv = 18.4) while adult females weighed 150 to 258 g (mean = 195.3, sd = 31.4, cv = 16.1). A length-weight scattergram for 72 *Atelomycterus fasciatus* with fitted exponential regression curve is presented as Figure 9B.

Fig.10. *Atelomycterus fasciatus*, two egg cases (67 mm long, 20 mm wide) removed from CSIRO H1299.10, 372 mm female. Vestibular end up, terminal end with horns and filaments down. Scale markings in mm. Photo by T. Carter.

Reproduction. *Atelomycterus fasciatus* is probably oviparous. Three adult females 352, 372 and 405 mm long in our sample were gravid and had a thick-walled egg case in each oviduct. These egg cases are similar to those of other oviparous scyliorhinids with single oviparity (Compagno, 1988), in which one egg case at a time is formed in the oviduct, and deposited on the substrate well before the embryo is ready to hatch.

The egg cases (Fig.10, removed from the uterus) are bright yellow in colour and measure 67 mm long from the center of the anterior or vestibular end to the bases of the horns at the terminal or posterior end, are 20 mm wide and 11 mm thick. In dorsoventral profile these egg cases have a truncated vestibular end, a pair of anterior convexities posterior to the vestibular end, a distinct waist or neck, a central convex body for the egg proper, a second posterior waist or neck, and a tapering terminal end that has two horns with twisted bases and curled, fine filaments. There are no vestibular horns on the cases, but these may form before the egg cases are laid.

Distribution and habitat. *Atelomycterus fasciatus* is a common offshore benthic shark on the continental shelf of Western Australia where it has been captured between Exmouth Gulf (22°S 114°15'E) and off the southern end of Eighty Miles Beach (20°S 120°E) (Fig.11). There are also single specimens of this species from the Arafura Sea (10°37'S 133°47'E), Northern Territory, and from the Gulf of Carpentaria (16°38'S 140°02'E) and Torres Strait (10°31'S 140°48'E) Queensland (Fig.11, inset map). Western Australian specimens were caught on sand and shelly sand bottoms with Frank & Bryce demersal trawls with a 30.5 m headline. Depths of capture were from 27 to 122 m, with most records shallower than 60 m.

Atelomycterus macleayi currently has a more extensive geographic range than *A. fasciatus*, with scattered records from Western Australia and the Northern Territory as well as Queensland (Whitley, 1940; Springer, 1979; Compagno, 1988; Paxton *et al.* 1989). The Indo-

West Pacific *A. marmoratus* is apparently absent from Australian waters but is nominally recorded from New Guinea (Springer, 1979; Compagno, 1988).

Atelomycterus macleayi is rarer in collections than *A. fasciatus*, which may reflect a habitat difference between these species. *Atelomycterus macleayi* may prefer reefs and other hard bottom habitats that are difficult to sample with demersal trawls, while *A. fasciatus* may prefer a soft mud and sand bottom. Only *A. fasciatus* was caught in the extensive series of soft-bottom trawl stations listed above.

Comparison with other species. *Atelomycterus macleayi* (Fig.12) and *A. marmoratus* (Fig.13) are readily distinguishable from *A. fasciatus* in external morphology and morphometrics, clasper structure, colouration, and vertebral counts (Table 3), and possibly differ in intestinal valve counts and cranial morphology. A summary of major morphometric differences with statistics are presented in Table 4 for 72 *A. fasciatus*, three *A. macleayi*, and nine *A. marmoratus*.

Atelomycterus macleayi and *A. marmoratus* have relatively shorter preoral snouts (POR) than *A. fasciatus*, with only a slight overlap (Fig.15A, Table 4). There may be negative allometry with POR in all three species, with smaller *A. macleayi* and *A. marmoratus* overlapping large *A. fasciatus*. Head length (HDL) is slightly greater in *A. fasciatus* than in the other two species, but with negative allometry in this species and *A. macleayi* and slight overlap between larger individuals of *A. fasciatus* and small *A. macleayi*.

Precaudal length (PCL) is slightly shorter in *Atelomycterus macleayi* and *A. marmoratus* than in *A. fasciatus* (Table 4). However, PCL is apparently positively allometric in *A. macleayi* and *A. fasciatus*, with small *A. fasciatus* overlapping large *A. macleayi* and *A. marmoratus* in this dimension.

Atelomycterus macleayi and *A. marmoratus* differ from *A. fasciatus* in their higher, rear-swept dorsal fins (Figs 12, 13, 14B), with the posterior margins vertical or slanting anteroventrally from the fin apices and the apices themselves usually more broadly rounded. The few *A. macleayi* examined have their dorsal fins more swept than in *A. marmoratus*. *Atelomycterus fasciatus* have the posterior margins of their dorsal fins slanting posteroventrally from their apices and the apices more narrowly rounded.

The anal fin is slightly larger in *Atelomycterus*

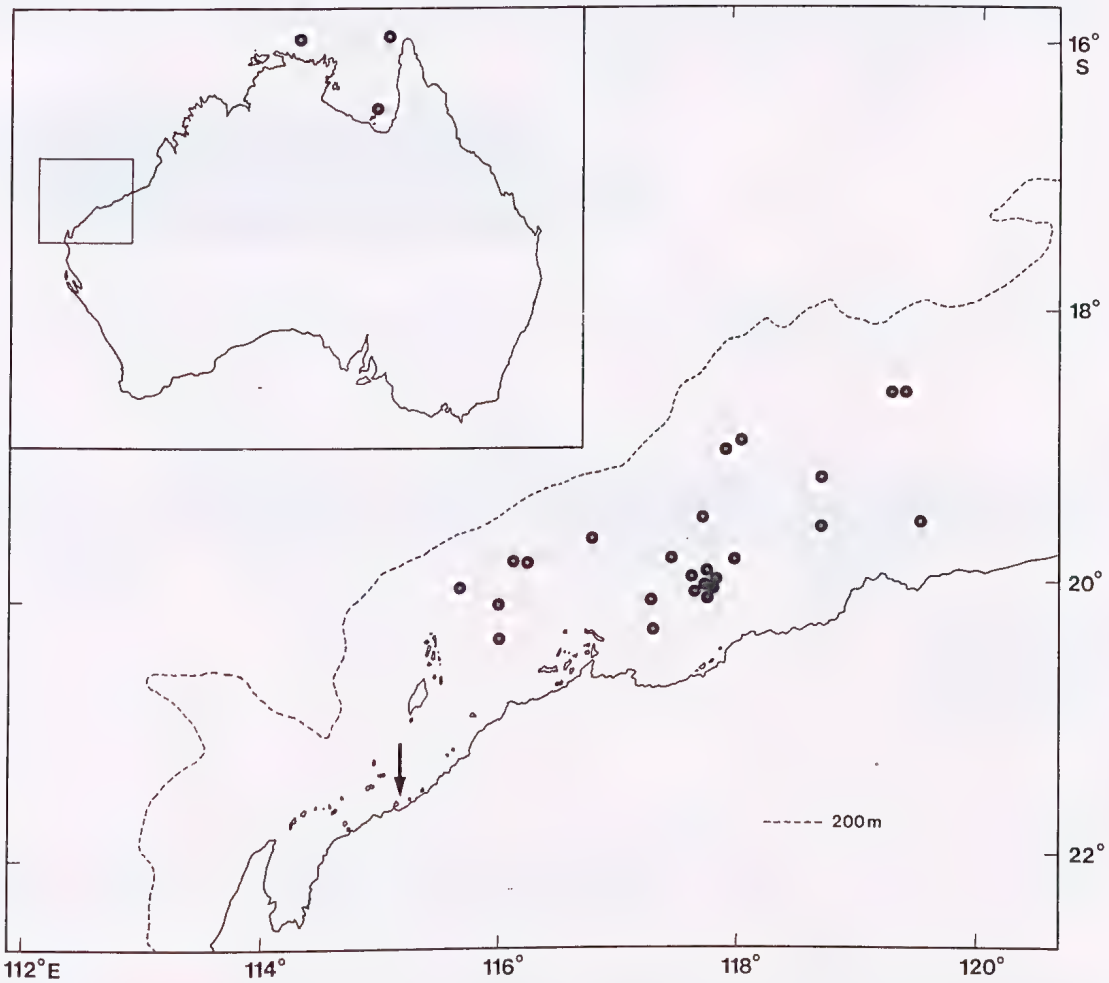

Fig.11. *Atelomycterus fasciatus*, distribution map. Inset: Continent with Western Australian range circumscribed by square, black dots show the records from the Arafura Sea, Gulf of Carpentaria and Torres Strait. Main map: enlargement of inset square with records (black dots) of specimens off the North West Shelf of Western Australia. Arrow points to area in which holotype was found. Map by P. White.

macleayi and *A. marmoratus* than in *A. fasciatus* (Table 4), with some overlap in height (ANH) and base length (ANB).

The three *Atelomycterus* species are sharply distinguished by the dimensions, external morphology and skeletal structure of their claspers. Adult males of *A. macleayi* have short, very stout claspers (Figs 12, 5C,D), *Atelomycterus marmoratus* has very long, attenuated claspers (Figs 13, 5E,F), while *A. fasciatus* is intermediate in having moderately stout and elongated claspers (Figs 1, 5A,B). Clasper dimensions do not overlap between the three species in our limited sample of adult males, including 17 *A. fasciatus*, two *A. macleayi* and three *A. marmoratus* (Table 4, Fig.14C). CLB as % CLO is diagnostic and reflects the different clasper shapes in the three species (Table 4).

The claspers of *Atelomycterus marmoratus* additionally differ from those of *A. fasciatus* and *A. macleayi* (Fig.5) in having the glans less than half the length of the clasper outer margin; a small, narrow anterior tab on the cover rhipidion; a small, narrow cover rhipidion, with its posterior end well anterior to the pseudopera and exorhipidion and far ahead of the rear end of the rhipidion; a low, subquadrate, striplike rhipidion; a much smaller exorhipidion and pseudopera that are well behind the cover rhipidion; a pseudosiphon aperture that is slightly longer than the cover rhipidion. The claspers of *A. marmoratus* additionally differ from those of *A. fasciatus* in being less tapered from apopyle to hypopyle and in having an exposed rhipidion (largely covered by the exorhipidion and cover rhipidion in *A. fasciatus*. The claspers of *A. macleayi* additionally differ from those of *A. fasciatus* in having a broader clasper glans with broad, blunt tip (narrower and tapering in *A. fasciatus*); a broader, more arcuate, exposed rhipidion; a shorter pseudosiphon less than half the length of the cover rhipidion.

The clasper skeleton of *A. macleayi* could not be studied, but that of *A. marmoratus* (Fig.15) differs of that of *A. fasciatus* (Fig.6) in numerous features, including

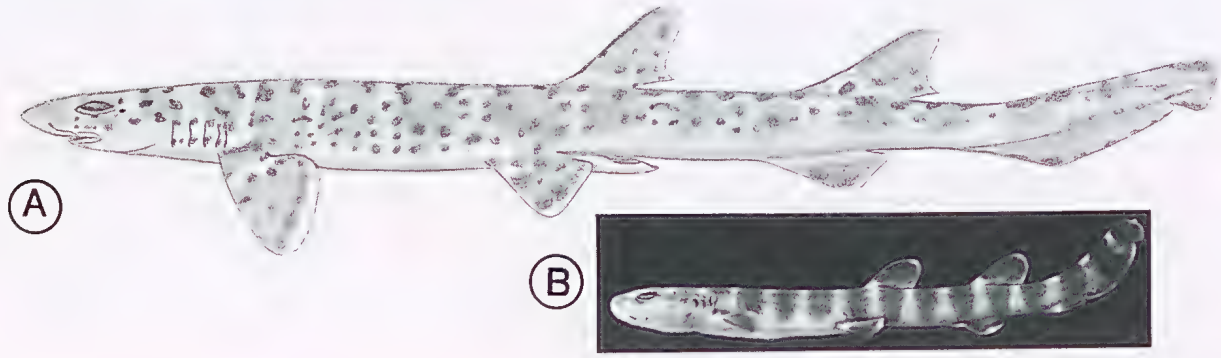

Fig.12. *Atelomycterus macleayi*. A, USNM 174070, 481 mm adult male, lateral view; B, WAM P8811, 100 mm hatchling male, lateral view, not to scale. Illustration and photograph by L.J.V. Compagno.

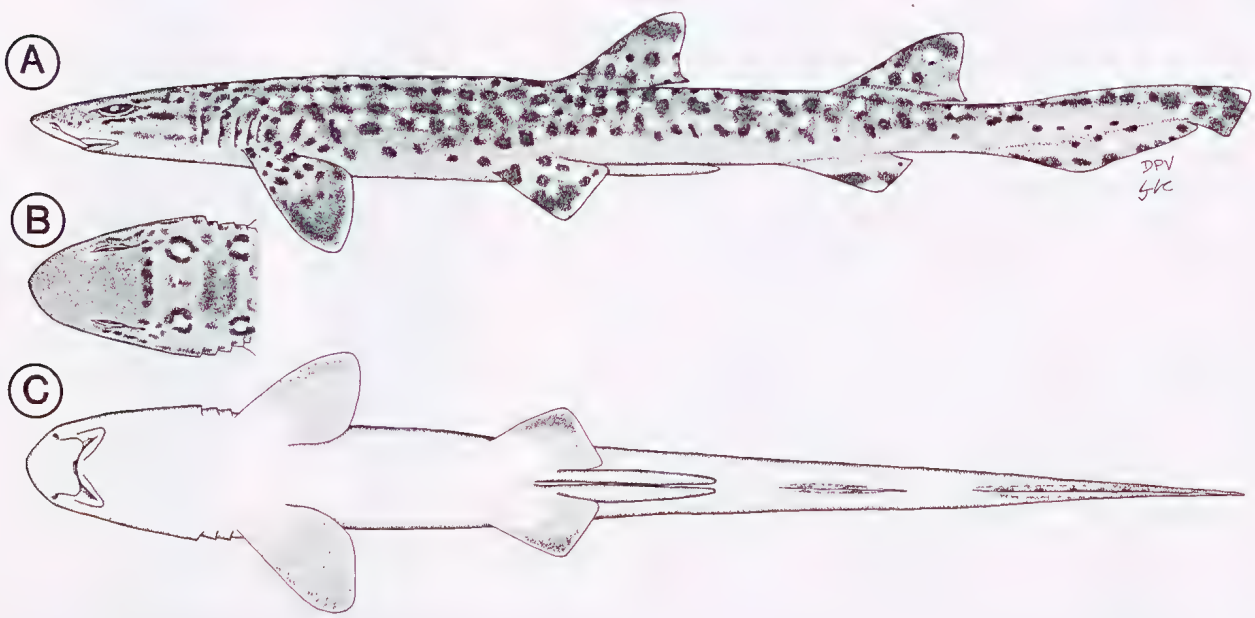

Fig.13. *Atelomycterus marmoratus*, SU 14182, 467 mm adult male. A, lateral view; B, dorsal view of head; C, ventral view. Illustration by D. Voorfelt and L.J.V. Compagno.

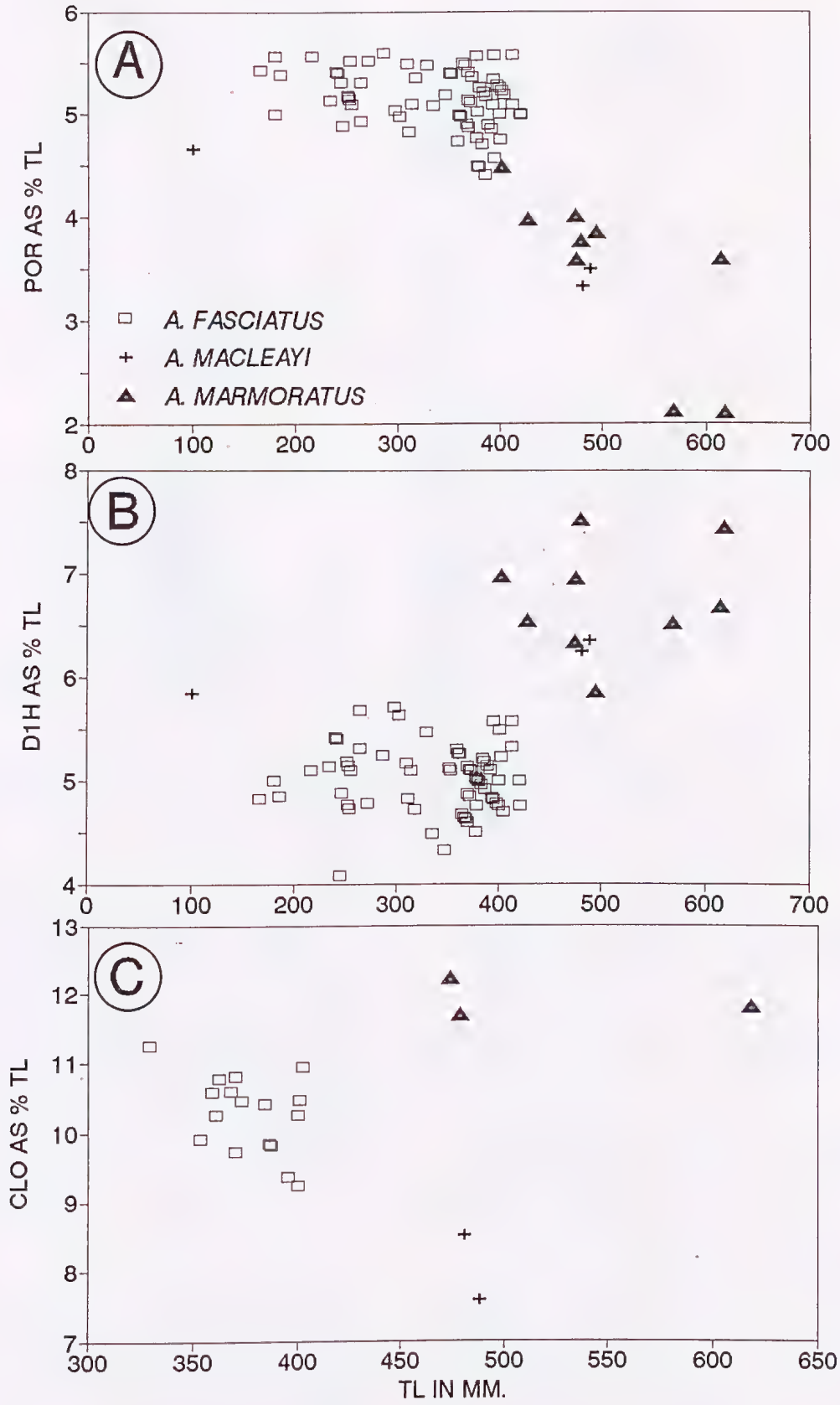

Fig.14. *Atelomycterus* species. Head proportions as percentages of total length versus total length (TL) in mm. *Atelomycterus fasciatus* – hollow squares; *Atelomycterus macleayi* – crosses; *Atelomycterus marmoratus* – filled triangles. A, preoral length (POR) as % TL versus TL; B, head length (HDL) as % TL versus TL; B, first dorsal height (D1H) as % TL versus TL; C, clasper outer length (CLO) as % TL versus TL.

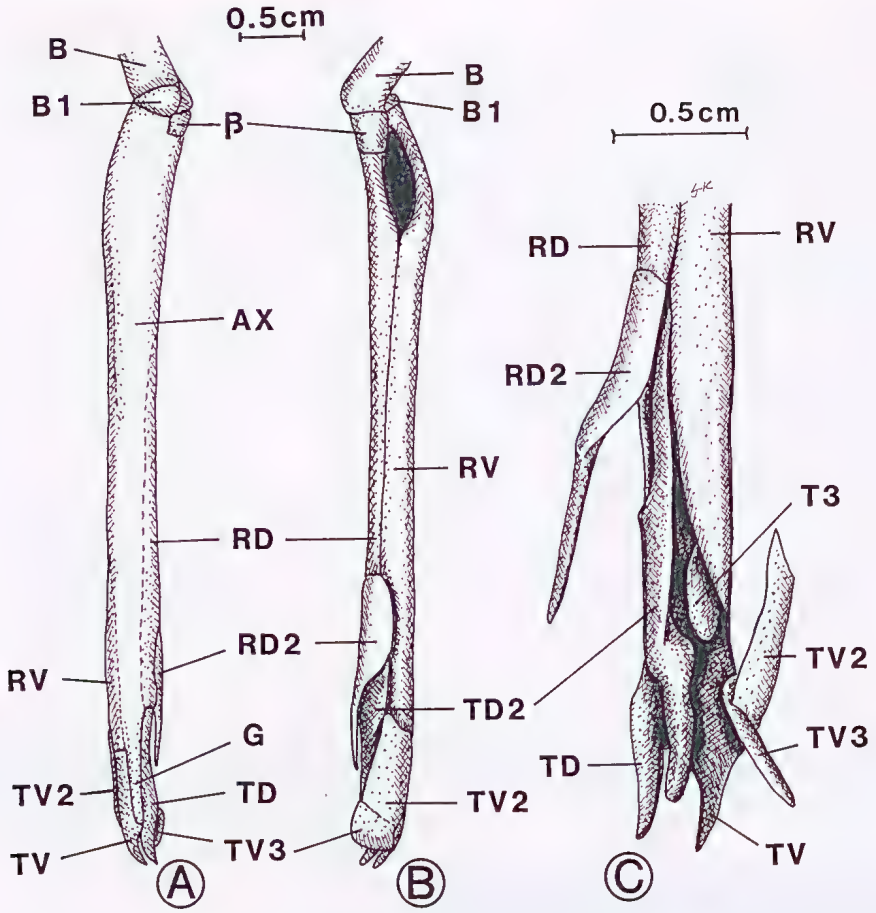

Fig.15. *Atelomycterus marmoratus*, clasper skeleton, SU 13659, 477 mm adult male, right side. A, ventral view; B, dorsal view, terminal cartilages not dilated; C, dorsal view of glans (twice size of B), terminal cartilages spread. Abbreviations as in Figure 6. Illustration by L.J.V. Compagno.

its more slender, parallel-sided clasper shaft (dorsal and ventral marginal cartilages distally splayed in *A. fasciatus*, giving the clasper shaft an elongated hourglass-shape), shorter appendix-stem, shorter dorsal and ventral terminal (TD and TV) cartilages, greatly elongated, attenuated accessory terminal dorsal (TD2) cartilage, and more distally attenuated accessory dorsal marginal (RD2) cartilage.

Intestinal valve counts may average slightly higher in *Atelomycterus macleayi* and *A. marmoratus* than in *A. fasciatus*, with some overlap between the latter two species. One *A. macleayi* counted had 15 turns, eight *A. marmoratus* had 13 to 14 turns (mean = 13.6, sd = 1.1, cv = 7.1), while 18 *A. fasciatus* had 11 to 13 turns (mean 12.2, sd = 0.6, cv = 5.3).

Adults and subadults of the *Atelomycterus* species are readily distinguished by colouration and colour pattern (Figs 1, 12, 13). *Atelomycterus macleayi* and *A. marmoratus* differ from *A. fasciatus* in having bolder colour patterns as adults, with numerous large and small dark brown or black spots on their bodies and fins, white tips on their dorsal and caudal fins, light-edged paired fins, and with saddles, where present, not extending onto the ventral surface of the tail or the abdomen. *Atelomycterus macleayi* additionally differs from *A. fasciatus* in having its saddles less well defined in adults, and of equal width (Fig.12A). *Atelomycterus fasciatus* alternates broad and narrow banding from the branchial region to the caudal base (Fig.1). *Atelomycterus marmoratus* is much darker than *A. fasciatus*, with the saddles obsolete and the dark brown to black spots enlarged and often merging to form dash and bar marks that bridge the saddle areas, and with the light ground colour reduced to large white spots on the sides and back.

Hatchling *A. fasciatus* and *A. marmoratus* have not been seen, but hatchling *A. macleayi* apparently differ from adults in having equal width, bold, simple, solid dark saddles without dark spots, but also having prominent white fin edges and tips (Fig.12B).

Atelomycterus marmoratus and *A. macleayi* have higher TC, PC and DP vertebral counts than *A. fasciatus*. In turn *A. macleayi* apparently has higher DP, PC and TC than *A. marmoratus*, and higher DP as % TC and DP/MP ratios than either *A. marmoratus* or *A. fasciatus* (Table 3).

Chondrocrania were not available for *Atelomycterus macleayi*, but comparison of the chondrocranium of a specimen of *A. marmoratus* (see Compagno, 1988:fig.13.2) with that of *A. fasciatus* (Fig.8) reveals

a few differences. *Atelomycterus marmoratus* has a complete rostral node, nasal apertures on the ventral surfaces of the nasal capsules (anterolateral in *A. fasciatus*), a rounded anterior fontanelle (subtrapezoidal in *A. fasciatus*), and laterally directed postorbital processes (posterolateral in *A. fasciatus*).

Atelomycterus macleayi and *A. marmoratus* apparently attain a larger size than *A. fasciatus*. Two adult males of *A. macleayi* are 481 and 488 mm long while three adult male *A. marmoratus* are 474, 479 and 615 mm long. A 428 mm female *A. marmoratus* is immature while a 475 mm female is adolescent and two females of 568 and 614 mm are gravid. A 614 mm adult female *A. marmoratus* weighed 750 g, approximately 2.9 times our heaviest adult female *A. fasciatus* (258 g).

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Table 1. *Atelomycterus fasciatus*. Proportional dimensions as percentages of total length for holotype and nine paratypes.

	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Coll.	WAM	CSIRO	CSIRO	WAM P	CSIRO	CSIRO	CSIRO	CSIRO	CSIRO	CSIRO
No.	P8629	CA4518	H1297-01	23838	CA4523	CA4524	H1294-01	CA3289	H1295-01	H1296-01
Sex/M	M 4	F 2	M 2	M 2	M 2	F ?	F 4	F ?	M 4	F 4
WT gm	163	32	34	38	53	85	205	172	218	258
TL mm.	370	216	234	251	264	318	372	395	400	413
PCL %	82.7	83.3	81.2	82.1	81.8	83.3	85.2	81.3	82.5	83.8
PRN	3.0	2.8	3.0	3.2	3.0	3.1	3.0	2.8	3.0	3.4
POR	5.1	5.6	5.1	5.2	4.9	5.3	5.1	4.6	5.3	5.6
POB	5.4	6.9	6.4	4.8	5.7	6.6	5.9	5.1	6.3	6.5
PSP	8.9	10.2	9.8	9.2	10.2	10.1	9.4	9.1	9.5	9.9
PGI	14.9	15.3	14.1	14.3	15.2	15.4	15.1	14.2	14.3	15.7
HDL	20.8	20.8	19.2	18.7	19.7	20.4	20.7	19.2	19.5	23.0
PP1	18.6	19.4	17.9	18.3	17.0	19.2	19.1	18.2	18.0	19.4
PP2	44.9	43.1	41.0	39.8	40.9	41.5	43.8	41.8	41.8	42.4
SVL	45.7	44.4	42.7	42.6	43.6	43.4	47.0	43.3	45.0	44.8
PAL	63.8	64.4	62.8	64.1	67.8	63.2	65.9	65.1	62.8	64.2
PD1	47.8	46.3	44.4	44.2	44.7	45.3	47.0	45.8	46.0	46.7
PD2	68.4	67.1	65.8	66.5	66.3	67.3	68.8	67.1	66.0	67.8
IDS	12.2	13.4	13.7	12.7	14.4	15.1	14.2	12.9	13.0	13.1
DCS	5.9	7.9	5.1	8.0	6.4	7.2	6.5	5.6	7.3	7.7
PPS	20.8	20.4	21.4	17.1	19.7	18.9	21.0	19.5	19.8	20.6
PAS	15.4	16.2	17.1	15.5	17.0	16.0	18.3	18.2	15.5	16.2
ACS	6.8	9.3	10.3	7.2	7.6	8.8	8.1	6.8	7.3	8.0
EYL	3.0	3.7	3.4	3.2	3.4	3.5	4.0	2.8	3.5	3.4
EYH	1.4	1.4	1.3	0.9	1.1	1.3	1.1	1.3	1.3	1.7
INO	6.5	6.9	6.0	6.0	6.8	6.6	7.0	6.1	6.3	6.1
NOW	2.7	2.3	2.1	2.0	1.9	2.2	2.4	2.3	1.8	2.9
INW	2.4	1.9	2.1	2.0	1.9	2.2	2.2	2.0	2.0	2.4
ANF	3.0	3.2	3.0	3.2	3.0	3.5	5.1	2.5	3.0	3.1
SPL	0.8	0.5	0.4	0.6	0.6	0.6	0.8	0.6	0.8	0.8
ESL	0.4	0.9	0.5	0.4	0.5	0.3	0.3	0.5	0.7	0.5
MOL	3.0	2.3	2.1	2.8	2.7	2.2	2.4	2.3	2.8	2.4
MOW	7.3	6.5	6.0	6.0	6.1	6.0	7.0	5.8	7.3	7.5
ULA	3.0	2.3	3.0	2.8	2.7	3.1	2.7	2.8	3.0	3.1
LLA	3.5	2.8	3.4	2.8	3.0	3.5	3.5	3.0	3.8	3.6
GS1	1.6	1.9	1.7	1.0	1.9	2.5	2.4	1.5	2.0	2.4
GS2	1.9	1.9	2.1	1.2	1.9	2.5	2.4	1.8	2.5	2.7
GS3	1.9	2.3	2.1	1.2	1.9	2.2	2.4	1.8	2.8	2.4
GS4	1.9	2.3	1.7	1.2	1.9	2.2	2.4	1.8	2.5	2.4
GS5	1.4	1.9	1.3	0.9	1.1	1.6	2.2	1.3	1.5	1.9
HDH	5.7	5.6	5.6	5.6	5.7	5.7	5.6	5.1	5.5	5.8
HDW	10.0	10.2	9.4	9.6	9.5	9.4	10.2	9.1	10.0	10.4
TRH	8.9	7.9	7.3	6.4	7.6	7.2	9.9	7.6	8.5	9.2
TRW	8.6	8.8	8.1	7.6	8.0	8.2	10.8	8.4	9.0	9.9
CPH	3.5	3.7	3.4	3.6	3.4	3.1	3.2	3.3	2.8	3.4
CPW	3.0	2.8	3.0	2.8	2.7	2.5	3.0	3.0	2.8	3.1
GIR	27.0	28.7	26.5	21.9	25.4	26.1	33.9	25.8	27.8	32.7
P1L	10.0	9.7	9.8	9.6	9.5	10.4	10.5	10.1	8.8	10.9
P1A	11.1	10.2	10.3	10.4	10.2	11.0	11.6	11.4	10.5	12.1
P1B	4.9	4.6	4.3	4.8	4.5	4.7	4.8	4.8	4.8	4.8
P1H	7.8	8.3	6.8	8.4	8.0	8.2	8.9	8.4	9.0	10.2
P1I	5.7	5.6	6.0	8.8	5.3	6.3	5.6	5.8	5.3	6.8
P1P	7.6	7.9	6.4	6.0	6.8	7.2	7.0	7.3	7.8	9.0
P2L	10.8	9.7	9.8	10.0	9.8	9.7	9.4	9.9	10.8	10.2
P2A	7.6	7.4	7.7	8.0	7.6	7.5	6.7	6.8	8.0	8.0
P2B	5.4	5.6	6.0	6.0	6.1	6.0	5.1	5.6	6.0	6.1
P2H	6.5	6.0	5.1	5.2	9.5	6.0	4.6	2.3	5.5	5.1
P2I	5.1	4.6	3.0	3.6	3.4	3.8	4.0	4.8	3.5	4.4
P2P	6.2	6.0	5.1	5.2	5.3	6.3	5.9	6.1	5.3	6.5
CLO	10.8	–	2.1	2.0	2.7	–	–	–	10.3	–

Table 1 (cont'd).

	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Coll.	WAM	CSIRO	CSIRO	WAM P	CSIRO	CSIRO	CSIRO	CSIRO	CSIRO	CSIRO
No.	P8629	CA4518	H1297-01	23838	CA4523	CA4524	H1294-01	CA3289	H1295-01	H1296-01
CLI	14.6	–	5.1	4.4	5.7	–	–	–	13.5	–
CLB	1.6	–	0.9	0.8	0.8	–	–	–	1.5	–
D1L	11.4	10.2	10.7	11.2	9.8	10.7	10.2	10.4	9.8	10.9
D1A	10.5	9.7	10.3	10.8	8.7	8.5	9.9	10.4	8.5	10.9
D1B	8.9	6.9	6.8	7.6	6.8	8.2	7.3	7.1	6.8	8.2
D1H	5.1	5.1	5.1	5.2	5.7	4.7	4.8	4.8	4.8	5.6
D1I	2.4	3.7	3.0	2.8	2.7	3.1	3.2	2.8	3.0	3.4
D1P	4.9	4.6	3.8	4.4	4.9	5.0	4.8	4.6	5.3	5.6
D2L	11.1	11.6	10.3	11.6	10.2	10.1	11.0	11.6	11.0	12.1
D2A	10.3	11.1	10.3	10.8	9.5	10.1	10.5	10.9	9.3	11.9
D2B	8.6	8.3	8.1	8.8	8.0	8.2	8.1	9.1	8.0	9.0
D2H	4.9	5.6	4.7	4.4	5.3	4.7	4.8	4.8	4.3	4.8
D2I	2.4	3.2	2.1	2.4	2.7	2.5	2.7	2.5	2.8	2.9
D2P	5.4	4.6	4.3	4.0	4.5	4.4	4.6	4.6	4.0	4.8
ANL	9.2	9.7	8.5	9.6	8.7	8.5	8.3	9.6	10.0	9.0
ANA	7.6	8.3	6.8	8.4	7.2	6.9	7.5	8.4	7.8	7.5
ANB	7.3	7.9	5.6	7.2	7.2	6.9	6.5	7.3	8.3	6.8
ANH	2.7	2.8	2.1	2.4	3.0	2.5	2.7	2.5	2.5	2.7
ANI	1.6	1.9	1.7	2.0	2.3	1.6	1.9	2.0	1.8	2.2
ANP	3.2	2.8	2.1	2.4	3.0	2.5	2.7	2.3	2.8	2.7
CDM	16.2	18.5	18.8	17.1	17.8	17.9	17.5	18.0	17.0	16.5
CPV	8.9	8.8	7.3	9.2	8.0	9.4	8.1	9.4	8.5	8.5
CPL+U	8.6	8.8	9.0	8.8	8.7	8.2	8.3	9.1	9.5	8.2
CST	2.7	2.8	3.4	3.6	3.0	2.8	3.2	3.0	2.3	2.7
CTR	4.9	4.6	4.3	4.0	4.5	3.5	3.8	4.6	4.0	4.4
CTL	4.6	4.6	4.7	4.8	4.9	4.1	4.3	4.8	4.0	5.1
DAO	3.5	3.2	3.8	3.2	3.4	4.4	2.7	2.5	4.0	2.2
DAI	4.6	3.7	6.0	4.8	3.8	5.0	4.3	4.3	3.8	4.8

Table 2. *Atelomycterus* species. Proportional dimensions as percentages of total length for three specimens of *A. macleayi* (including the holotype) and nine *A. marmoratus*.

	A. macleayi			*A. marmoratus*								
Coll.	AMS	WAM	USNM	SU	LACM	SU	SU	SU	SPA	SU	BPBM	SU
No.	I5269 (HOLO)	P8811	174070	40095	37431	14182	13689	13659	UNC.	13563	29851	13562
Sex/M	M 4	M 2	M 4	F 2	F 2	M 4	F 3	M 4	F ?	F 4	F 4	M 4
TL mm	488	101	481	402	428	474	475	479	495	568	614	618
PCL %	79.3	75.2	79.0	78.6	79.4	79.3	80.0	77.7	80.8	80.1	80.0	77.8
PRN	2.0	2.7	1.9	2.2	2.3	2.1	1.7	2.1	1.8	3.9	1.8	3.6
POR	3.5	4.7	3.3	4.5	4.0	4.0	3.6	3.8	3.8	2.1	3.6	2.1
POB	4.3	5.6	4.0	5.5	4.4	5.5	5.1	5.2	4.2	4.8	3.9	4.9
PSP	6.8	8.8	7.5	8.7	7.7	8.6	8.0	8.1	7.7	8.1	8.0	7.9
PGI	12.1	15.4	12.5	12.9	12.1	13.3	13.3	12.9	12.5	13.9	12.7	12.3
HDL	17.0	19.6	17.7	18.2	17.8	18.1	17.9	17.5	18.0	19.2	17.6	18.0
PP1	16.4	17.4	16.6	16.9	16.1	15.8	16.8	15.9	16.6	18.5	16.4	16.2
PP2	–	39.5	–	37.1	36.4	36.9	37.5	36.3	40.4	38.7	37.9	37.5
SVL	41.0	41.6	40.7	39.8	40.4	40.1	38.1	38.8	42.6	40.5	40.1	39.8
PAL	–	58.4	–	57.7	60.0	61.2	60.4	58.5	62.6	62.0	58.8	59.2
PD1	43.0	44.6	43.7	41.3	40.2	43.9	41.3	40.9	46.7	40.7	43.8	40.5
PD2	–	62.4	–	62.7	62.4	63.7	62.1	62.0	67.1	63.2	63.7	60.7
IDS	12.7	10.3	13.5	11.9	12.4	14.8	15.6	14.6	14.1	13.2	14.0	12.3
DCS	6.6	5.0	6.4	5.7	6.5	6.8	7.8	7.1	6.3	4.9	7.7	5.5
PPS	18.4	17.6	18.5	16.7	16.6	16.0	18.3	14.6	17.2	17.3	19.2	16.7
PAS	15.4	12.6	17.9	14.2	15.7	19.0	18.1	17.1	16.6	19.7	17.3	16.5
ACS	7.8	7.3	7.3	5.7	7.9	6.8	7.2	7.5	7.9	4.9	7.8	6.1
EYL	2.5	2.4	2.5	3.2	2.8	3.0	3.2	3.1	2.4	3.0	2.8	3.1
EYH	0.6	0.2	0.8	1.2	0.7	1.7	1.3	1.3	1.2	1.2	0.8	1.1
INO	4.9	7.6	5.6	5.2	6.1	5.3	5.3	5.6	6.1	5.8	5.0	5.5
NOW	1.8	1.8	1.5	1.7	1.9	2.3	2.1	1.9	2.8	2.1	2.0	1.9
INW	1.4	1.8	1.9	1.2	1.6	1.7	1.3	1.3	4.2	1.6	1.8	1.3
ANF	2.5	2.6	2.5	3.0	2.8	2.7	2.7	2.7	2.0	3.0	2.6	2.8
SPL	0.4	0.3	0.4	0.5	0.7	1.1	0.8	1.0	0.6	1.1	0.8	1.0
ESL	–	0.3	0.4	0.5	–	0.6	0.8	0.6	0.4	0.7	0.5	0.6
MOL	1.8	2.0	2.9	2.2	2.6	2.5	2.1	2.7	2.8	2.3	2.3	2.4
MOW	5.7	7.7	5.6	6.2	5.4	5.9	6.1	6.3	5.9	6.2	5.9	6.1
ULA	2.5	2.2	2.5	3.2	2.8	2.7	2.7	3.3	2.4	3.0	2.9	2.9
LLA	2.9	3.1	3.3	3.5	2.8	3.4	3.4	3.8	3.2	3.3	3.1	3.4
GS1	1.8	1.1	2.1	2.0	2.6	2.5	1.7	2.1	2.2	2.3	2.4	2.1
GS2	1.8	1.1	2.1	2.2	2.6	2.5	2.1	2.1	2.2	2.6	2.9	2.3
GS3	2.5	1.1	2.1	2.2	2.6	2.5	2.1	2.1	2.0	2.6	2.8	2.4
GS4	1.6	0.8	1.9	2.0	2.1	2.1	2.1	1.9	1.8	2.6	2.4	2.3
GS5	1.4	0.7	1.5	1.5	1.6	1.5	1.7	1.5	1.2	2.1	1.8	1.8
HDH	4.9	6.5	–	5.2	6.8	4.9	5.9	5.2	4.6	5.6	5.0	5.5
HDW	6.8	10.3	–	9.0	10.3	8.6	9.3	9.4	8.5	8.6	8.5	9.1
TRH	–	8.4	6.9	7.7	–	7.6	6.3	8.4	7.7	9.3	7.3	7.8
TRW	–	4.6	8.1	7.0	–	7.6	8.6	6.9	8.9	8.3	7.3	7.6
CPH	3.5	4.8	4.2	4.0	4.2	3.6	3.6	3.3	3.4	3.7	3.7	3.7
CPW	2.7	3.0	2.7	2.7	2.8	3.0	3.2	2.9	3.0	2.8	3.1	3.2
GIR	–	24.8	–	–	–	25.3	24.2	25.1	28.1	29.6	26.1	24.3
P1L	9.2	8.9	8.5	9.5	9.8	9.5	8.2	9.6	10.7	9.3	12.2	9.1
P1A	11.3	10.8	9.8	11.4	11.7	11.0	10.5	10.6	10.7	11.3	11.4	10.8
P1B	4.1	3.7	3.7	4.0	4.9	4.4	3.8	4.4	3.6	4.6	3.9	4.4
P1H	6.8	7.0	7.3	9.7	9.1	8.9	9.5	7.3	7.3	8.6	9.3	10.0
P1I	4.7	4.7	4.8	5.0	4.9	4.9	4.2	5.6	6.1	3.7	5.2	4.5
P1P	–	6.5	8.5	7.2	–	6.3	7.4	7.7	8.1	6.3	8.6	7.8
P2L	9.0	7.9	9.6	10.0	9.8	9.5	9.3	10.2	7.9	5.3	9.6	9.9
P2A	7.4	6.5	7.1	8.7	8.2	7.6	7.8	8.1	7.5	10.0	7.7	8.6
P2B	5.5	5.2	6.0	6.5	6.1	6.1	5.5	6.1	5.7	6.7	6.0	7.0
P2H	5.7	5.2	5.4	5.2	6.3	4.6	5.5	5.6	6.1	5.5	5.4	5.7
P2I	3.7	3.7	2.5	4.0	4.0	3.8	3.6	4.4	3.2	4.0	3.9	3.7
P2P	–	5.6	5.4	5.0	–	5.5	5.1	5.2	6.5	5.8	5.7	5.8

Table 2 (cont'd).

	A. macleayi			*A. marmoratus*								
Coll.	AMS	WAM	USNM	SU	LACM	SU	SU	SU	SPA	SU	BPBM	SU
No.	I5269 (HOLO)	P8811	174070	40095	37431	14182	13689	13659	UNC.	13563	29851	13562
CLO	7.6	1.2	8.5	–	–	12.2	–	11.7	–	–	–	13.8
CLI	11.5	3.0	11.6	–	–	15.8	–	15.2	–	–	–	16.2
CLB	–	0.6	1.9	–	–	1.3	–	1.3	–	–	–	1.1
D1L	11.3	9.7	9.8	11.4	11.0	9.7	11.8	9.8	10.7	11.4	8.5	11.8
D1A	12.9	12.0	11.4	13.4	12.9	11.0	12.8	11.5	11.5	12.7	9.6	12.6
D1B	9.0	6.6	6.7	8.7	7.7	7.0	9.3	7.3	7.5	8.6	6.2	8.3
D1H	6.4	5.8	6.2	7.0	6.5	6.3	6.9	7.5	5.9	6.5	6.7	7.4
D1I	2.3	2.4	3.1	3.0	3.3	3.4	2.7	2.9	4.0	3.5	3.1	3.1
D1P	–	5.7	–	5.2	–	5.3	5.7	6.3	6.1	5.6	6.4	6.3
D2L	11.7	10.4	11.4	12.4	11.9	11.4	10.9	11.5	10.7	12.3	11.2	13.4
D2A	12.9	12.2	12.7	13.7	12.4	12.9	11.6	12.1	11.1	13.4	10.6	14.4
D2B	9.2	7.5	8.3	9.7	8.9	8.9	8.8	9.2	7.3	10.4	8.1	11.0
D2H	5.7	6.3	6.2	5.5	5.6	5.5	5.9	6.3	6.3	5.8	6.0	6.6
D2I	2.5	2.3	3.1	3.0	3.0	2.7	2.3	2.7	2.6	2.6	2.4	2.6
D2P	–	5.3	–	4.2	–	4.4	4.6	5.4	5.3	4.6	5.4	5.5
ANL	12.7	12.3	11.0	11.4	11.4	11.2	10.3	11.3	9.1	11.3	11.4	12.0
ANA	9.4	9.4	8.5	10.0	9.3	8.9	8.2	9.2	7.9	9.2	8.6	10.5
ANB	10.5	9.2	8.5	9.5	9.1	8.6	8.8	9.0	7.9	9.3	9.1	9.9
ANH	3.1	3.2	3.1	3.5	3.3	3.4	3.2	3.5	3.2	3.0	3.4	3.7
ANI	2.3	1.8	2.5	2.2	2.3	2.3	1.9	3.3	2.0	1.9	2.4	2.4
ANP	–	4.6	4.2	3.5	–	3.8	3.6	3.8	3.4	3.9	4.2	4.2
CDM	20.1	21.2	19.8	20.6	21.0	19.6	19.6	22.3	19.8	17.6	19.5	21.7
CPV	8.8	8.3	8.5	11.2	8.6	9.7	8.6	10.0	7.1	10.0	8.5	9.9
CPL+U	11.3	13.6	12.5	10.7	10.5	11.0	10.7	11.1	11.9	10.7	11.2	12.1
CST	3.1	3.0	2.9	3.5	4.0	3.4	3.2	4.2	3.2	3.5	3.4	4.0
CTR	4.1	4.3	4.4	4.0	4.7	3.4	3.6	3.8	4.6	4.2	4.4	4.5
CTL	4.3	4.4	4.6	5.2	5.8	4.9	5.1	5.6	5.5	5.1	5.5	6.0
DAO	4.5	4.7	2.1	3.7	4.2	2.5	3.4	3.3	3.4	2.1	4.4	3.2
DAI	3.1	2.5	1.9	3.5	4.2	2.7	3.6	4.4	3.4	2.6	3.7	3.4

Table 3. *Atelomycterus* species. Vertebral counts and ratios for specimens of *A. fasciatus*, *A. macleayi* and *A. marmoratus*.

A. fasciatus	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
WAM-P8629	370	43	60	54	103	157	27.3	38.2	34.3	1.4	1.3	123	68
WAM-P23838	251	42	60	47	102	149	28.1	40.2	31.5	1.4	1.1	167	83
CSIRO CA3289	395	41	62	47	103	150	27.3	41.3	31.3	1.5	1.1	115	78
CSIRO H1295-01	400	42	61	53	103	156	26.9	39.1	33.9	1.5	1.3	143	68
CSIRO H1294-01	372	42	62	52	104	156	26.9	39.7	33.3	1.5	1.2	133	60
CSIRO CA4524	318	41	61	–	102	–	–	–	–	1.5	–	130	81
CSIRO H1296-01	413	39	62	50	101	151	25.8	41.0	33.1	1.6	1.3	114	67
CSIRO H1297-01	234	41	66	–	107	–	–	–	–	1.6	–	139	90
CSIRO CA4523	264	40	61	–	101	–	–	–	–	1.5	–	140	75
CSIRO CA4518	216	41	69	–	110	–	–	–	–	1.7	–	163	62
CSIRO H1294-02	286	42	62	–	104	–	–	–	–	1.5	–	139	67
CSIRO CA4514	389	46	61	54	107	161	28.5	37.8	33.5	1.3	1.2	133	56
CSIRO H1297-03	353	44	60	50	104	154	28.5	38.9	32.4	1.4	1.1	125	78
CSIRO H1300-02	366	42	60	–	102	–	–	–	–	1.4	–	132	69
CSIRO H1307-01	310	43	62	–	105	–	–	–	–	1.4	–	119	66
CSIRO H1095-01	335	45	55	–	100	–	–	–	–	1.2	–	124	68
CSIRO CA4519	253	44	65	–	109	–	–	–	–	1.5	–	115	65
CSIRO CA4517	359	45	59	50	104	154	29.2	38.3	32.4	1.3	1.1	126	65
	range	39	55	47	100	149	25.8	37.8	31.3	1.2	1.1	114	56
		46	69	54	110	161	29.2	41.3	34.3	1.7	1.3	167	90
	mean	42.4	61.6	50.8	103.9	154.2	27.7	39.4	32.9	1.5	1.2	132.1	70.2
	SD	1.8	2.9	2.5	2.7	3.6	1.0	1.2	1.0	0.1	0.1	14.3	8.6
	CV	4.2	4.7	5.0	2.6	2.3	3.6	3.0	3.0	7.4	5.3	10.8	12.2
	N	18	18	9	18	9	9	9	9	18	9	18	18

A. macleayi	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
USNM 174070	481	47	85	51	132	183	25.6	46.4	27.8	1.8	1.1	119	71

A. marmoratus	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
GVF NO NO.	443	47	70	61	117	178	26.4	39.3	34.2	1.5	1.3	140	78
LACM NO NO.	491	46	72	57	118	175	26.2	41.1	32.5	1.6	1.2	131	77
SU 13689	475	44	72	49	116	165	26.6	43.6	29.6	1.6	1.1	122	68
SU 13659	479	46	67	54	113	167	27.5	40.1	32.3	1.5	1.2	121	69
SU 13563	568	45	73	46	118	164	27.4	44.5	28.0	1.6	1.0	115	68
SU 14182	474	46	70	52	116	168	27.3	41.6	30.9	1.5	1.1	132	81
SU 40095	402	44	73	55	117	172	25.5	42.4	31.9	1.7	1.3	132	78
	range	44	67	46	113	164	25.5	39.3	28.0	1.5	1.0	115	68
		47	73	61	118	178	27.5	44.5	34.2	1.7	1.3	140	81
	mean	45.4	71.0	53.4	116.4	169.9	26.8	41.8	31.4	1.6	1.2	127.4	74.1
	SD	1.0	2.0	4.6	1.6	4.9	0.7	1.7	1.9	0.1	0.1	7.9	5.1
	CV	2.3	2.8	8.7	1.4	2.9	2.5	4.1	6.0	4.6	7.5	6.2	6.8
	N	7	7	7	7	7	7	7	7	7	7	7	7

Table 4. Statistical summary for certain morphometrics of *Atelomycterus* species. Clasper proportions are from adult males. Note that samples of each species are not exactly equivalent and that mean, standard deviation and coefficient of variation of allometric proportions are sensitive to growth-related variation and hence to differing size composition of individuals in the three samples.

	Range	Mean	SD	CV	N
PCL % TL					
A. fasciatus	77.8-86.1	83.1	1.5	1.8	71
A. macleayi	75.2-79.3	77.9			3
A. marmoratus	77.7-80.8	79.3	1.0	1.3	9
POR % TL					
A. fasciatus	4.4-5.6	5.1	0.3	5.5	71
A. macleayi	3.3-4.7	3.8			3
A. marmoratus	2.1-4.5	3.5	0.8	22.4	9
HDL % TL					
A. fasciatus	18.4-21.3	20.0	0.7	3.4	71
A. macleayi	17.0-19.6	18.1			3
A. marmoratus	17.5-19.2	18.0	0.5	2.6	9
D1H % TL					
A. fasciatus	4.1-5.7	5.0	0.3	6.2	70
A. macleayi	5.8-6.4	6.1			3
A. marmoratus	5.9-7.5	6.8	0.5	7.4	9
ANB % TL					
A. fasciatus	4.5-10.1	7.0	0.7	10.6	71
A. macleayi	8.5-10.5	9.4			3
A. marmoratus	7.9-9.9	9.0	0.5	5.8	9
ANH % TL					
A. fasciatus	1.6-3.3	2.6	0.3	11.3	71
A. macleayi	3.1-3.2	3.1			3
A. marmoratus	3.0-3.7	3.4	0.2	6.2	9
CLO % TL					
A. fasciatus	9.3-11.2	10.3	0.5	5.2	17
A. macleayi	7.6-8.5				2
A. marmoratus	11.7-12.2	11.9			3
CLI % TL					
A. fasciatus	12.7-14.7	13.7	0.6	4.1	17
A. macleayi	11.5-11.6				2
A. marmoratus	13.8-20.9	16.8			3
CLB % TL					
A. fasciatus	1.4-1.8	1.6	0.1	6.7	17
A. macleayi	1.9				1
A. marmoratus	1.1-1.3	1.2	0.1	4.9	3
CLB/CLO x 100					
A. fasciatus	12.7-17.4	15.2	1.2	7.6	17
A. macleayi	22.0				1
A. marmoratus	9.6-10.7	10.2			3

Galeus gracilis n.sp., a New Sawtail Catshark from Australia, with Comments on the Systematics of the Genus *Galeus* Rafinesque, 1810 (Carcharhiniformes: Scyliorhinidae)

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ABSTRACT. *Galeus gracilis* n.sp. (Scyliorhinidae: Pentanchinae: Galeini) is described from the uppermost slope of Western Australia and the Northern Territory. It is the second recognised member of its genus from Australian waters. This small, slender-bodied *Galeus* is distinguished from the 12 other species in the genus by a combination of proportional dimensions, tooth-row counts, clasper morphology, pectoral-fin radial counts, vertebral counts, intestinal valve counts, chondrocranial morphology, and colouration. It is closest to three Japanese species: *G. eastmani*, *G. longirostris* and *G. nipponensis*. *Galeus gracilis* is compared in detail to *G. boardmani* from southern Australia, which differs from it in numerous features.

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The sawtail catsharks, genus *Galeus* Rafinesque, 1810 (Scyliorhinidae: Pentanchinae: Galeini), were most recently reviewed by Compagno (1988), who recognised 11 species following the work of Cadenat (1959), Springer (1966, 1979), Springer & Wagner (1966), Nakaya (1975), Cadenat & Blache (1981), Compagno (1984), and Muñoz-Chapuli & Ortega (1985). While Compagno's review was in press, Tachikawa & Taniuchi (1987) described a 12th valid species from Japan.

The geographic distribution of *Galeus* species is spotty and disjunct. The known species cluster by region and show considerable sympatry in the eastern Atlantic and western North Pacific (Compagno, 1988):

Western North Atlantic: *Galeus arae* (Nichols, 1927), South Carolina south to Caribbean and Colombia.

Eastern Atlantic: *Galeus melastomus* Rafinesque, 1810, Faroes and Norway south to Mediterranean and Senegal; *G. murinus* (Collett, 1904), Iceland and Faroes; *G. atlanticus* (Vaillant, 1888), Morocco and Spain; *G. polli* Cadenat, 1959, southern Morocco to central Namibia.

Australia: *Galeus boardmani* (Whitley, 1928), south coast from Western Australia to New South Wales.

Western North Pacific: *Galeus eastmani* (Jordan & Snyder, 1904), Japan, possibly Vietnam and the East

China Sea; *G. sauteri* (Jordan & Richardson, 1909), Taiwan, possibly Japan and Philippines; *G. schultzi* Springer, 1979, Philippines; *G. nipponensis* Nakaya, 1975 and *G. longirostris* Tachikawa & Taniuchi, 1987, Japan.

Eastern Pacific: *Galeus piperatus* Springer & Wagner, 1966, northern Gulf of California.

Recent offshore trawl surveys on the outer continental shelves and upper slopes of Australia (Gloerfelt-Tarp & Kailola, 1984; Davis & Ward, 1984; Sainsbury *et al.*, 1985; Gorman & Graham, 1985; Williams, 1987) has produced a wealth of scyliorhinid catsharks along with many other sharks and bony fishes. Compagno (1984, 1988) noted the presence of an undescribed species of *Galeus* off Western Australia that is very different from the Australian species *G. boardmani* but is closer to the western North Pacific *G. eastmani*, *G. nipponensis* and *G. longirostris*. It differs from these species in vertebral counts, e xternal and cranial morphology, morphometrics and colouration; we describe it below as *Galeus gracilis* n.sp.

The purpose of this paper is to describe this new species and to compare it with the other known species of the genus.

Terminology and Abbreviations

The terminology for external structures, chondrocrania, vertebrae and dentition follows Compagno (1970, 1988). For vertebrae, an additional abbreviation PC is introduced for precaudal (monospondylous + diplospondylous precaudal) vertebral counts. The abbreviations and methods of measuring follow the FAO system of Compagno (1984), except that the measurement MOL (mouth length) was incorrectly shown in the diagram (Compagno, 1984: 12) as extending from the lower symphysis to the mouth corners; it should be from the *upper* symphysis to the mouth corners. Also, TL is used for total length and PCL for precaudal length (following general usage in ichthyology) instead of TOT and PRC. The abbreviations for measurements in this account include: TL (TOT) – total length; PCL (PRC) – precaudal length; PRN – prenarial length; POR – preoral length; POB – preorbital length; PSP – prespiracle length; PGI – pregill (prebranchial) length; HDL – head length; PP1 – prepectoral length; PP2 – prepelvic length; SVL – snout-vent length; PAL – preanal length; PD1 – pre-first dorsal length; PD2 – pre-second dorsal length; IDS – interdorsal space; DCS – dorsocaudal space; PPS – pectoral-pelvic space; PAS – preanal space; ACS – anal-caudal space; EYL – eye length; EYH – eye height; INO – interorbital width; NOW – nostril width; INW – internarial width; ANF – anterior nasal flap length; SPL – spiracle length; ESL – eye-spiracle length; MOL – mouth length; MOW – mouth width; ULA – upper labial furrow length; LLA – lower labial furrow length; GS1 – first gill opening height; GS2 – second gill opening height; GS3 – third gill opening height; GS4 – fourth gill opening height; GS5 – fifth gill opening height; HDH – head height; HDW – head width; TRH – trunk height; TRW – trunk width; CPH – caudal peduncle height; CPW – caudal peduncle width; GIR – girth; P1L – pectoral length; P1A – pectoral anterior margin; P1B – pectoral base; P1H – pectoral height; P1I – pectoral inner margin; P1P – pectoral posterior margin; P2L – pelvic length; P2A – pelvic anterior margin; P2B – pelvic base; P2H – pelvic height; P2I – pelvic inner margin; P2P – pelvic posterior margin; CLO – clasper outer length; CLI – clasper inner length; CLB – clasper base width; D1L – first dorsal length; D1A – first dorsal anterior margin; D1B – first dorsal base; D1H – first dorsal height; D1I – first dorsal inner margin; D1P – first dorsal posterior margin; D2L – second dorsal length; D2A – second dorsal anterior margin; D2B – second dorsal base; D2H – second dorsal height; D2I – second dorsal inner margin; D2P – second dorsal posterior margin; ANL – anal length; ANA – anal anterior margin; ANB – anal base; ANH – anal height; ANI – anal inner margin; ANP – anal posterior margin; CDM – dorsal caudal margin; CPV – preventral caudal margin; CPL+U – combined lower and upper postventral caudal margin; CST – subterminal caudal margin; CTR – terminal caudal margin; CTL – terminal caudal lobe; DAO – second dorsal-anal origin; DAI – second dorsal-anal insertion. NBL is for nasobasal length, the distance from the base of the medial rostral cartilage to the occipital centrum of the chondrocranium. Pectoral radial counts include all radials and combine free mesopterygial and metapterygial radials with the fused proximal segments of the propterygial and first two mesopterygial radials, which are counted as three additional radials (Fig.5). This is unlike the method of Muñoz-Chapuli & Ortega (1985), who counted only the free radials.

Abbreviations and prefixes for field, accession, and catalogue numbers follow Leviton *et al.* (1986) and Compagno (1988), or have been coined specially: Annnn, 0nn, nnnn or Enn – RV *Africana* station, cruise, and block or experimental station number, Sea Fisheries Research Institute, Cape Town; AMS – Australian Museum, Sydney; CAS – California Academy of Sciences, San Francisco; CSIRO CA and CSIRO H – CSIRO Marine Laboratories, Hobart, Tasmania; DAE – D.A. Ebert field number; ISH – Institut fur Seefischerei, Hamburg; LJVC – L.J.V. Compagno catalogued collection; ORE – RV *Oregon* station number, US National Marine Fisheries Service; QM – Queensland Museum, Brisbane; RUSI – J.L.B. Smith Institute of Ichthyology, Grahamstown; SO – CSIRO RV *Soela* station number; SAM – South African Museum, Cape Town; SB – RV *Silver Bay* station number, US National Marine Fisheries Service; SU – Stanford University Division of Systematic Biology fish collection – now housed at CAS; WAM, Western Australian Museum, Perth. Abbreviations for statistics: cv – coefficient of variation (100 x standard deviation/mean); n – number of specimens; sd – standard deviation.

All tables are listed in the Appendix.

Schyiorhinidae Gill, 1862

Pentanchinae Smith & Radcliffe, 1912

Galeini Fowler, 1934

Comments. Compagno (1988) presented discussions and definitions of the subfamilies and tribes of Scyliorhinidae. The Pentanchinae includes the tribes Pentanchini and Galeini, of which the Galeini is the most diverse in genera.

Galeus Rafinesque, 1810

Galeus Rafinesque, 1810: 13. Type species *Galeus melastomus* Rafinesque, 1810, by subsequent designation of Fowler, 1908: 53.

Definition. Slender-bodied to moderately stout, cylindrical to compressed, long-headed catsharks with firm skin and well-calcified dermal denticles. Stomach not inflatable. Tail moderately long, length from vent to lower caudal origin about 0.4-0.8 of snout-vent length. Snout moderately long, rounded-parabolic or angular in dorsoventral view, usually pointed in lateral view; snout without greatly enlarged ampullal pores. Nostrils enlarged but with incurrent and excurrent apertures only partly open to exterior; anterior nasal flaps small, low, angular, well separated from the midline and ending in front of mouth. No nasoral grooves. Eyes dorsolateral or nearly lateral on head, with subocular grooves narrow to non-existent. Mouth angular or semiangular, teeth prominently exposed in ventral view of head. Labial furrows on both jaws moderately long, uppers ending well behind lower symphysis. Branchial region short, gill slits lateral on head. Posterior teeth not differentiated at distal ends of dental bands. Two dorsal fins present, about equal-sized; origin of first dorsal varying from over pelvic-fin midbases to over their insertions; second dorsal-fin origin over the last half of the anal-fin base. Inner margins of pelvic fins not fused over claspers in adult males of most species (*G. boardmani*, an exception). Claspers without an anterior tab on cover rhipidion; pseudosiphon short; clasper tip without a papillose brush. Anal fin large and more or less elongated, larger than dorsal fins and variably smaller or larger than pelvic fins; anal origin varying from close to pelvic-fin insertions to far behind pelvic bases, and insertion varying from well anterior to adjacent to lower caudal-fin origin. Caudal fin more or less elongated, over a fifth of total length in adults, with crests of enlarged denticles on the dorsal and sometimes preventral caudal margins. Supraorbital crests absent from cranium. Vertebral centra weakly calcified, with intermedialia hardly developed and without diagonal calcifications. Total vertebral counts 115-150. Colour pattern of dark saddles and blotches variably present or absent, no small dark or light spots.

For comprehensive definitions, synonymies and discussions of the nomenclature, systematics, and relationships of this genus see Springer (1979) and Compagno (1984, 1988).

Comparative Material

Galeus arae. All from western North Atlantic: FLORIDA STRAITS: SB 2420, 305 mm TL adult male, 24°14'S 81°24'W, South of Key West. GULF OF MEXICO, off Mississippi Delta: SB 3515, 2 females, 275, 280 mm TL; SU 66815, 8 females, 213, 216, 227, 229, 234, 246, 248, 260 mm TL, and 233 mm TL immature male; 29°33'N 88°38'W. CARIBBEAN SEA: ORE 3627, 4 adult males, 255, 270, 277, 278 mm TL, 16°50'N 81°21'W, off Jamaica; ORE 1870, 284 mm TL female, 16°39'N 82°29'W, off Honduras; SU 66814, 5 females, 206, 206, 215, 232, 250 mm TL, 2 immature males, 198, 205 mm TL, 3 adult males, 270, 273, 275 mm TL, 14°08'N 81°55'W, east of Cayos Miskito, Nicaragua. NO DATA: LJVC-0075, 315 mm TL adult female (cranium in Fig.13A); LJVC-0076, 319 mm TL adult female; LJVC-0077, 310 mm TL adult female; LJVC-0078, 315 mm TL adult female (2 skeletonised); RUSI 6105, 267 mm TL adolescent male, head dissected.

Galeus boardmani. AUSTRALIA: AMS IA2483, 542 mm TL adult male, HOLOTYPE of *Pristiurus (Figaro) boardmani* Whitley, 1928, Montague Island, NSW (radiographed); AMS I22807-020, 225 mm immature male, 252 mm female, 176 mm female, continental shelf of north-western Australia, 200 m; CSIRO H989.04, 432 mm adult male (skeletonised), SO5/84/63, 21 Oct. 1984, 43°41'S 145°46'E.

Galeus eastmani. JAPAN, Honshu: SU 7740, 336 mm TL female, Izu, HOLOTYPE of *Pristiurus eastmani* Jordan & Snyder, 1904; SU 35469, 344 mm TL adult male, Sagami Sea.

Galeus melastomus. EASTERN NORTH ATLANTIC: ISH 223/75, 472 mm TL adult female, 43°28'N 09°16'W; LJVC-0454, 680 mm TL adult female, south-west of Lousy Bank; SU 20604, 380 mm TL immature female, Naples, Italy.

Galeus murinus. EASTERN NORTH ATLANTIC: ISH 769/64, 530 mm TL adult female, 65°13'N 27°49'W; ISH 41/65, 495 mm TL adult male, 64°07'N 27°16'W.

Galeus polli. NAMIBIA: RUSI 6258, 215 mm TL immature female; SAM-29460, 311 mm TL adult female; SAM-uncat. 313 mm TL adult male and 339 mm TL adult female with 7 late fetuses, 5 males, 67-84 mm TL, 2 females, 80-86 mm TL. *Africana* A3439 039 E17, 390 mm female, (skeletonised, cranium as Fig.13H), 24°28.6'S 13°24.6'E, 308 m; SAM-uncat., *Africana* A8370 069 E17 (cancelled station), 291 mm TL adolescent male, 375 mm adult female, 23°19.1'S 13°9.9'E, 407 m. SAM-uncat., *Africana* cruise 069, aborted station (after A8397), 5 adult females, 350, 364, 375, 385, 390 mm TL, 25°50.9'S 13°9.9'E, 411 m. *Africana* A6948 059 E17, 311 mm TL late adolescent male, 4 adult males, 310, 317, 326, 329 mm TL, 4 females, 349, 361, 363, 387 mm TL, 27°31.6'S 14°31.3'E.

Galeus sauteri. TAIWAN: SU 21261, 4 adult males, 364, 367, 367, 370 mm TL, Takao, SYNTYPES of *Pristiurus sauteri* Jordan & Richardson, 1909; CAS Acc. 1971-VI: 11, 382 mm TL subadult female, CAS Acc. 1972-III: 14, 383 mm TL adult male and 450 mm TL adult female, all from Taiwan Straits; DAE 881605, 317 mm TL adolescent male, 169 mm immature male and 2 immature females, 110-131 mm, Tachi fish market. PHILIPPINE ISLANDS: CAS 34132, 2 females, 301-303 mm TL, Batangas Province, Batangas Bay, east of Talaga (identification provisional).

Galeus schultzi. PHILIPPINE ISLANDS, LUZON, BATANGAS

PROVINCE, BALAYAN BAY: CAS 33783, 177 mm TL female, south of Cape Santiago; CAS 34556, 2 immature males, 165-182 mm TL, south-east of Pagapas Bay; CAS 34852, 143 mm TL immature female and 155 mm TL immature male, south-east of Pagapas Bay; CAS 34861, 147 mm TL immature male, south of Cape Santiago.

Galeus gracilis n.sp.

Slender sawtail catshark

Figs 1-10, 13E

Type material. HOLOTYPE, CSIRO H1208.01, 335 mm TL adult female, Jan. 1988, upper slope north of Melville Island, NT, 9°49'S 130°15'E, 290 m.

PARATYPES, CSIRO CA3304, 317 mm TL adult female, SO2/82/45, 13 Apr. 1982, upper slope north of Dampier Archipelago, WA, 18°48'S 116°51'E, 403 m; CSIRO CA4477, SO1/84/17, 329 mm TL adult male, and CSIRO CA4478, 333 mm TL adult male (dissected), both from SO1/84/17, 31 Jan. 1984, upper slope north of Dampier Archipelago, WA, 18°41'S 117°04'E, 453 m.

Non-type material. QM 120676, 150 mm TL, 9°S 144°E; WAM 28098, 330 mm TL adult male, 1983, 18°44'S 116°59'E.

Diagnosis. *Galeus* with a long, parabolic snout, snout tip narrowly rounded. Preoral length about 6.4-7.8% TL and 0.9-1.0 times mouth width; prenarial snout 0.9-1.3 times eye length. Eyes dorsolateral on head, with narrow but well-developed subocular ridges. Eyes small, length 3.2-3.3% TL in adults; eye length 5.7-6.7 in head length. Mouth moderately large and long, broadly arched, width 7.0-8.1% TL. Labial furrows moderately long, not confined to mouth corners. Teeth

Fig.1. *Galeus gracilis* n.sp., CSIRO H1208.01, 335 mm TL adult female holotype. A, lateral view; B, underside of head, enlarged. Photos by T. Carter.

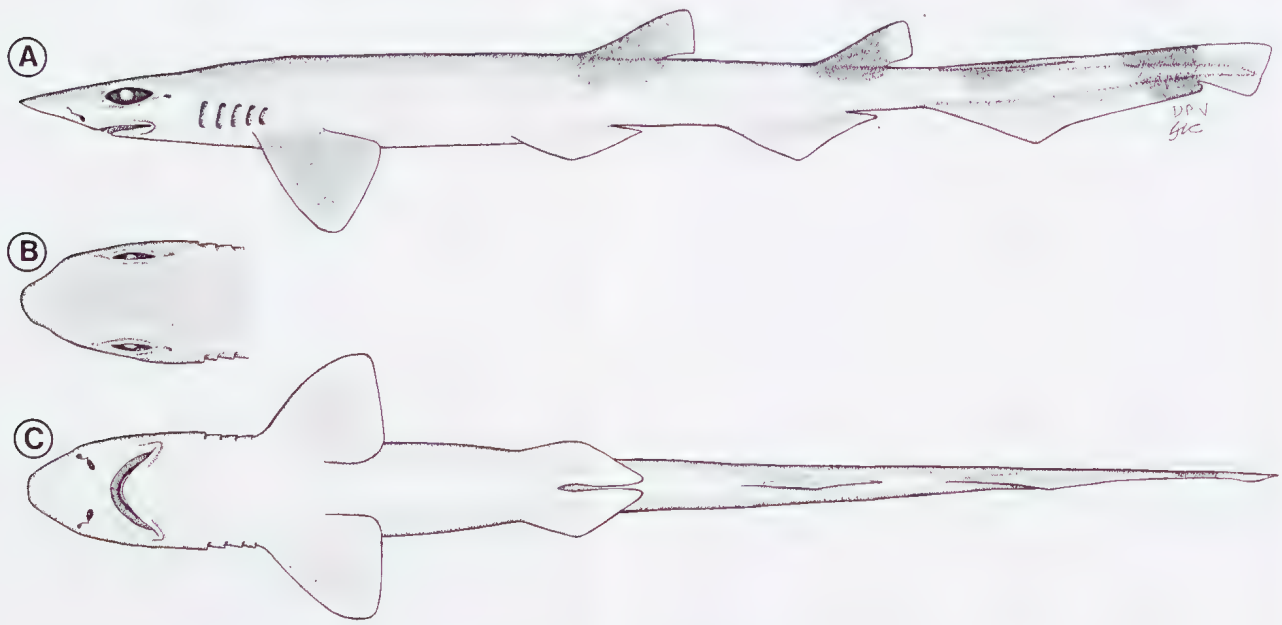

Fig.2. *Galeus gracilis*, CSIRO CA3304, 317 mm TL adult female paratype. A, lateral view; B, dorsal view of head; C, ventral view. Illustration by D. Voorfelt and L.J.V. Compagno.

in 54-57/54-62 rows. Body and precaudal tail slender. Caudal peduncle not greatly compressed, width 1.1-1.4 in height; peduncle elongated, anal-caudal space 0.5-0.7 of anal-fin base. Abdomen long, pectoral-pelvic space 14.3-16.0% TL and 0.7-0.9 of head length in adults. Pelvic-anal space long, 0.8-1.0 of anal base. Claspers moderately long in adult males, clasper outer length 10.3-10.8% TL, distal tips extending well behind pelvic fin rear tips but falling just short of anal-fin origin. Claspers tapering rearwards from base, not cylindrical or hourglass-shaped, tips narrow, pointed, not strongly twisted or truncated. Clasper tips with prominent groups of enlarged, anteriorly pointing hooked denticles on their lateral and mesial surfaces. Clasper glans very long, about 0.6 length of clasper from apopyle to tip. Cover rhipidion small but well developed. Pseudosiphon present and well developed. Exorhipidion large, bulbous, with group of enlarged, anteriorly pointing hooked denticles on outer lateral surface, but without transverse clasper hooks on mesial edge. Pectoral fin moderately large and broad, anterior margin 9.7-11.0% TL. Pectoral-fin skeleton with 16 radials; 2 proximal segments of mesopterygial radials fused together. Pelvic fins small, low, angular. Anal fin very short, base 10.5-11.5% TL and 1.1-1.2 in interdorsal space; anal origin under anterior half of interdorsal space; anal height 3.0-3.7 in base. No subcaudal crest of enlarged denticles on preventral caudal-fin margin. Total centra 130-134, MP centra 33-36, DP centra 41-44, precaudal centra 74-78. Intestinal valve with 6-7 turns. Chondrocranium with long rostrum, medial rostral cartilage 39% of NBL. Bases of lateral rostral cartilages narrow-spaced. Nasal capsules very large and obliquely elongated, anterior margins at approximately a right angle to each other. Anterior fontanelle small and nearly round, not longitudinally elongated. Cranial roof moderately broad and arched. Preorbital processes small. Suborbital shelves with nearly straight, posteriorly divergent edges. Postorbital processes small and directed anterolaterally. Otic capsules small. Occipital condyles prominently exserted. Size small, adults of both sexes 312-335 cm long. Mode of reproduction unknown. Adults light gray above, with well-defined dark saddles on body below first and second dorsal fins, on upper caudal fin base, and across caudal at base of terminal lobe, not highlighted with light lines; dorsal fins dusky with light distal webs; mouth lining blackish.

Etymology. From Latin *gracilis*, slender, gracile, in reference to the slim proportions of this little shark.

Description. Proportional dimensions as percentages

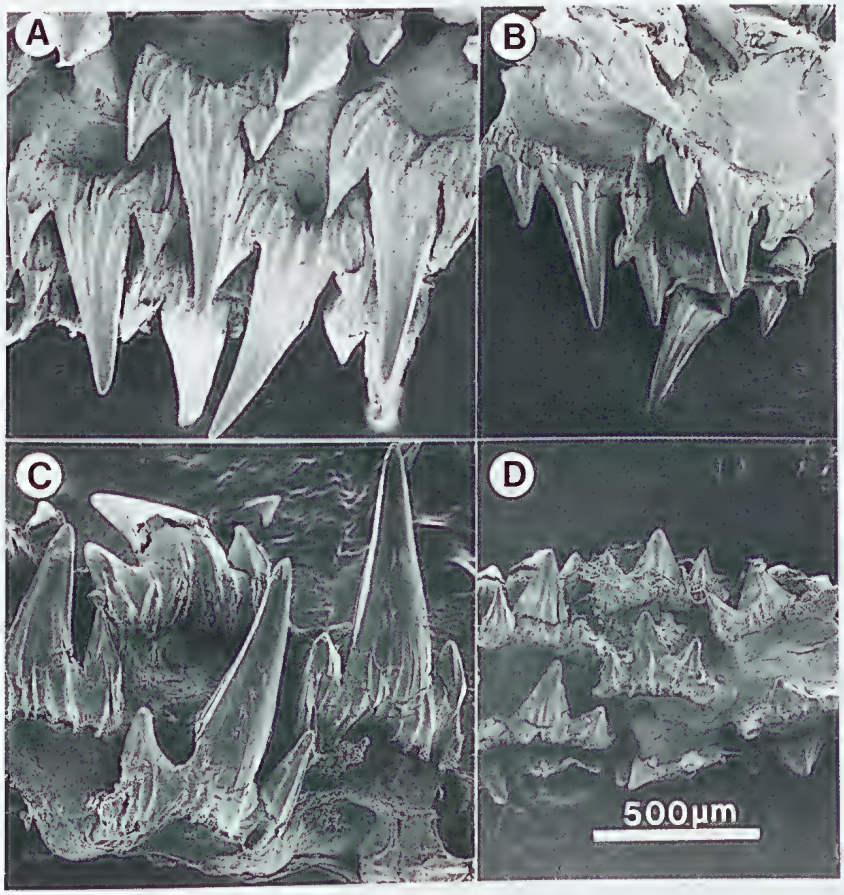

Fig.3. *Galeus gracilis*, scanning electron micrographs of groups of representative teeth from left side, labial views with roots imbedded in dental membrane, CSIRO CA4478, 333 mm TL adult male paratype. A-B, upper teeth; C-D, lower teeth. A, teeth from near upper symphysis; B, teeth from near end of upper dental band; C, teeth from near lower symphysis; D, teeth from near end of lower dental band. Scale bar (for all photographs) = 0.5 mm or 500 microns. Photos by A.J. Rees.

of total length for the holotype and 3 paratypes are presented in Table 1.

Head short, length 1.1 times pectoral-pelvic space. Head fairly narrow but strongly depressed, with a flat trapezodial cross-section at eyes. Outline of head in lateral view nearly straight or slightly convex in front of pectoral fins; in dorsoventral view head has a broad parabolic outline anterior to gill openings. Preoral snout 0.9-1.0 times mouth width, with a narrowly rounded tip in dorsoventral view, noticeably indented anterior to nostrils; snout bluntly pointed in lateral view, nearly straight or slightly convex above and below.

External eye opening with prominent anterior and posterior eye notches; eyes moderately large and spindle-shaped, eye length 5.7-6.7 in head length and 1.8-3.7 times eye height. Eyes dorsolateral on head, with lower edges distinctly medial to horizontal head rim in dorsal view, subocular ridges narrow but strong. Nictitating lower eyelids of rudimentary type, with shallow, scaled subocular pouches and secondary lower eyelids free from upper eyelids.

Spiracles small, length 2.8-5.5 in eye length, spiracles 0.2-0.4 eye lengths behind and below posterior eye notch. First 3 or 4 gill openings about equally high, fifth 0.4-1.2 height of third; third 9.4-23.6 in head and 0.3-0.6 of eye length. Gill openings straight to slightly concave, gill filaments not visible from outside. Upper ends of gill openings slightly below lower edges of eyes, gill openings not elevated on dorsolateral surface of head. No gill-raker papillae on gill arches.

Nostrils with small elongated incurrent apertures without posterolateral keels, small, bluntly angular anterior nasal flaps, small, low mesonarial flaps, large oval excurrent apertures, low posterior nasal flaps. Nostrils well in front of mouth, with anterior nasal flaps far in front of upper symphysis. Nostril width 1.0-1.3 in internarial space, 1.4 in eye length, 0.4-0.9 in third gill opening width.

Mouth broadly arched, moderately large and short, mouth width about 0.7 of head width at mouth corners, 2.5-3.1 in head length; mouth length 1.8-2.5 in mouth width. Lower symphysis falling short of upper symphysis, teeth prominently exposed in ventral view. Tongue moderate-sized, flat and rounded, filling most of floor of mouth. Maxillary valve narrow, width about 0.2 of eye diameter, highly papillose. No large buccal papillae on floor and roof of mouth behind maxillary valve. Palate with buccopharyngeal denticles confined to a crescent band covering its anterior third, denticles present on gill arches but absent from tongue and floor of pharynx behind tongue. Labial furrows moderately long, anterior ends of uppers well behind lower symphysis. Labial cartilages well developed.

Teeth in 57/62 (CSIRO CA3304), 54/54 (CSIRO CA4477), and 54/62 (CSIRO CA4478) rows in the 3 paratypes, 2-3/3-4 series functional. Teeth not arranged in diagonal files, no toothless spaces at symphysis. Teeth not highly differentiated in upper and lower jaws and along jaws, tooth row groups include medials (M) and anteroposteriors (AP). Tooth formula (CSIRO CA4478) is:

$$\text{Left} \quad \frac{\text{AP27 M1 AP29}}{\text{AP30 M3 AP28}} \quad \text{Right}$$

Sexual heterodonty present but weak, teeth slightly enlarged and with longer cusps in adult males. Height of upper anterolateral tooth near symphysis 0.37% of total length in adult male (CSIRO CA4477, 1.2 mm) but 0.22% in adult female (CSIRO CA3304, 0.7 mm). Upper teeth slightly narrower crowned and with longer transverse ridges than lowers near symphysis. Medials weakly differentiated at symphysis, slightly smaller than adjacent anteroposteriors. Anteroposteriors in both jaws have strong erect to semioblique (in upper posterior teeth) cusps and usually one strong high cusplet on either side. All teeth with strong basal ledges and grooves, strong transverse ridges notching

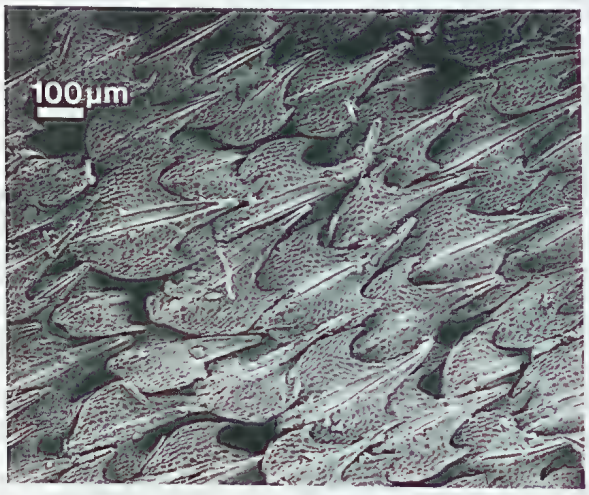

Fig.4. *Galeus gracilis*, scanning electron micrograph of lateral trunk denticles from back of CSIRO CA4478, 333 mm TL adult male paratype. Scale bar = 0.1 mm or 100 microns. Photo by A.J. Rees.

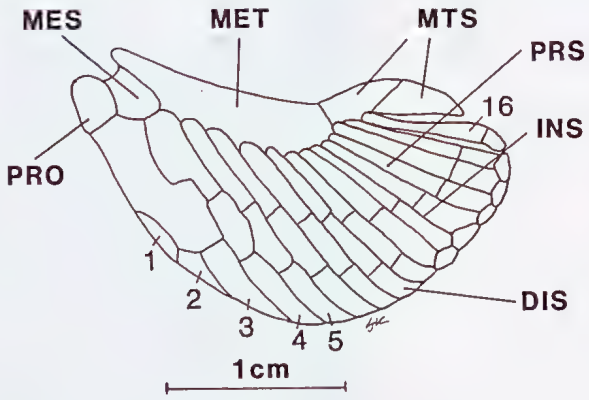

Fig.5. *Galeus gracilis*, pectoral fin skeleton from CSIRO CA4478, 333 mm TL adult male paratype. Numbers show convention for counting pectoral fin radials. This specimen has 16 radials, including one on the propterygium, three on the mesopterygium, and 12 metapterygial radials. Abbreviations: DIS – distal radial segments; INS – intermediate radial segments; MES – mesopterygium; MET – metapterygium; MTS – metapterygial segment (axis); PRO – propterygium; PRS – proximal radial segments. Illustration by L.J.V. Compagno.

basal ledges, extending onto cusps and cusplets partway to their tips, and low, flat roots. Gradient monognathic heterodonty well developed in anteroposterior teeth; distally anteroposteriors become smaller, with thicker and (in upper teeth) more oblique cusps, and lower cusplets. On most distal upper teeth cusp is shifted slightly distal on crown foot, with sometimes 2 mesial cusplets, but neither upper nor lower teeth are comb-shaped. Tooth histological type orthodont, with a definite pulp cavity.

Body slender, trunk vertically oval in section at first dorsal-fin base, length of trunk from fifth gill openings to vent 1.0-1.2 times head length. No predorsal, interdorsal or postdorsal ridges on midline of back, no postanal ridge between anal-fin base and lower caudal-fin origin; no lateral ridges on body. Caudal peduncle moderately long, low, slightly compressed, cylindrical-tapering and without lateral keels, caudal peduncle height at second dorsal-fin insertion 1.1-1.4 of width there, 0.9-1.4 in dorsal-caudal space.

Lateral trunk denticles with flat, elongated teardrop-shaped crowns about 1.6 times as long as wide, with all surfaces except medial ridges covered with prominent reticulated depressions. Crown with a strong single or narrow double medial ridge that extends entire length of crown onto the long, strong, narrow medial cusp; medial cusp about as long as the rest of the crown. Lateral cusps well developed, narrow, acute, and about a fourth as long as medial cusp, lateral ridges absent.

Pectoral fins broad and rounded-triangular, not falcate, with broadly convex anterior margins, broadly rounded apices, nearly straight posterior margins, broadly rounded free rear tips, convex inner margins, and broad bases. Pectoral-fin anterior margin 0.9-1.0 times pectoral-fin length. Pectoral fins nearly 3 times area of first dorsal fin. Origins of pectoral fins below fourth gill opening or below interspace between fourth and fifth gill openings. Apex of pectoral fin anterior to its free rear tip when fin is elevated and adpressed to body.

Pectoral fin skeleton with radials extending about 0.4 of pectoral anterior margin length into fin. Radials almost entirely divided into 3 segments, except for last metapterygial radial and possibly propterygial radial, which are bisegmental; longest distal segment 0.9 times length of its proximal segment. Pectoral-fin skeleton tribasal, propterygium probably with a single radial, mesopterygium probably with 3 radials, metapterygium

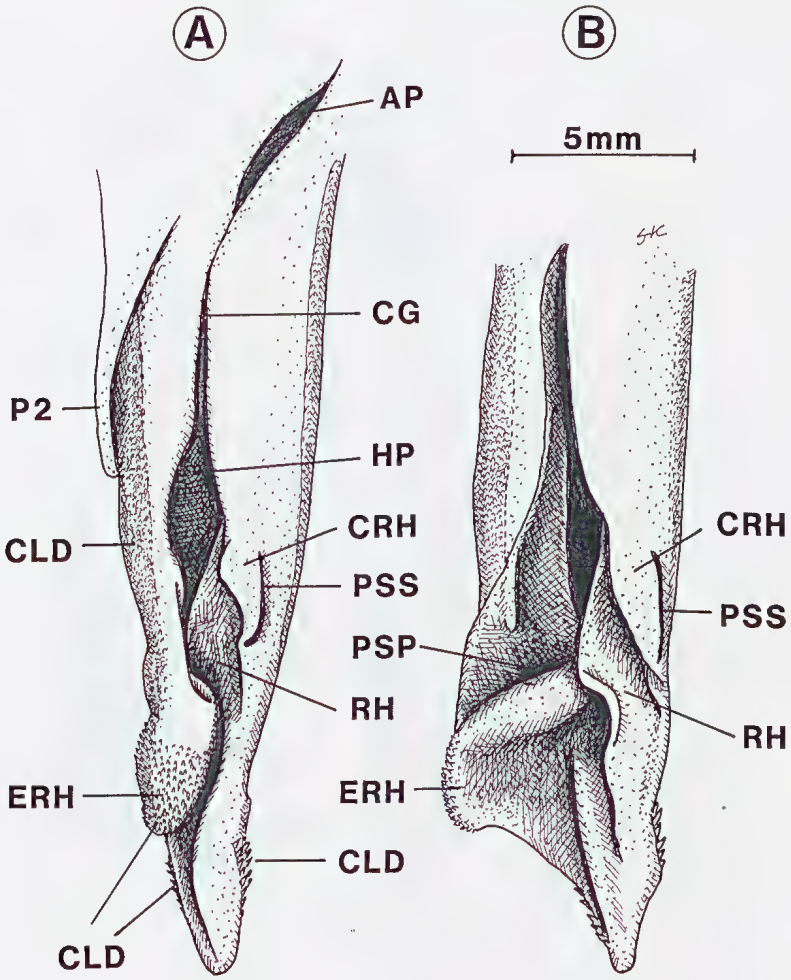

Fig.6. *Galeus gracilis*, left clasper in dorsal view from CSIRO CA4478, 333 mm TL adult male paratype. A, glans not dilated; B, glans spread. Abbreviations: AP – apopyle; CG – clasper groove; CLD – clasper denticles (including enlarged denticles on exorhipidion and clasper tip); CRH – cover rhipidion; ERH – exorhipidion; HP – hypopyle; P2 – pelvic fin; PSP – pseudopera; PSS – pseudosiphon; RH – rhipidion. Illustration by L.J.V. Compagno.

with 10 radials on basal segment, 2 on metapterygial axis; total radial count 16. Propterygium short, broad and subquadrate, not distally elongated. Proximal segments of propterygial radial and first mesopterygial radial forming a fused plate with intermediate segments of first and second mesopterygial radials. Mesopterygium and metapterygium not separated by an elongated fenestra. Mesopterygium short, subpentagonal, slightly elongated distally in the axes of its radials. Proximal segments of second and third mesopterygial radials fused together. Metapterygial basal segment triangular, elongated diagonal to the axes of its radials; metapterygial axis long, bisegmental, with length about 0.7 of metapterygial basal segment.

Pelvic fins low, broadly triangular; pelvic anterior margins 0.4-0.7 of pectoral-fin anterior margins; pelvic area slightly less than anal-fin area. Pelvic-fin anterior margins nearly straight or slightly convex, apices broadly rounded, posterior margins nearly straight, free rear tips attenuated and relatively pointed, inner margins not fused over claspers in adult males but with a slight fold of skin stretching between them.

Claspers relatively long but stout at base, convex and strongly tapering on lateral edge, clasper glans long and with slightly twisted, long, narrow tip. Claspers extending well behind pelvic-fin free rear tips in adult males but falling in front of anal-fin origin by only 0.2 of anal base. Most of dorsal surface of clasper naked except exorhipidion, and lateral and mesial margins; greatly enlarged clasper denticles with anteriorly directed cusps in two groups on mesial and lateral surfaces of clasper tip behind exorhipidion (HD2 and HD3 of Tachikawa & Taniuchi, 1987), these forming sawlike rows. Exorhipidion strongly differentiated, originating behind cover rhipidion, with a broad, blunt apex, moderately long base, and partly free posterior end. Exorhipidion covered with a third group of large, anteriorly directed denticles (HD1 of Tachikawa & Taniuchi, 1987) but lacking specialised clasper hooks. Pseudopera weakly developed below anterior end of exorhipidion and just behind posterior end of cover rhipidion, very shallow. No envelope present anterior to hypopyle. Rhipidion

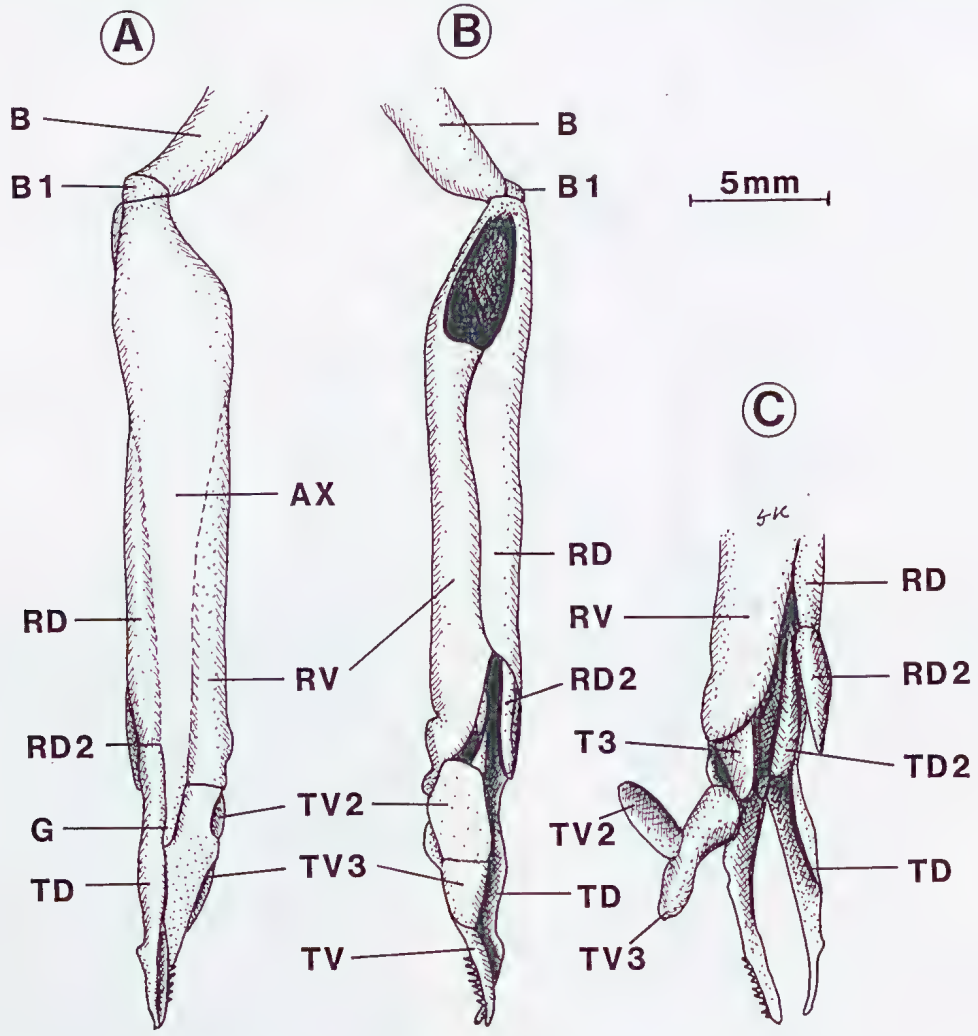

Fig.7. *Galeus gracilis*, clasper skeleton, CSIRO CA4478, 333 mm TL adult male paratype. A, ventral view; B, dorsal view, terminal cartilages not dilated; C, dorsal view of glans, terminal cartilages spread. Abbreviations: AX – axial cartilage; B – basipterygium; B1 – intermediate segment; G – end-style; RD – dorsal marginal cartilage; RD2 – accessory dorsal marginal cartilage; RV – ventral marginal cartilage; T3 – accessory terminal cartilage; TD – dorsal terminal cartilage; TD2 – dorsal terminal 2 cartilage; TV – ventral terminal cartilage; TV2 – ventral terminal 2 cartilage; TV3 – ventral terminal 3 cartilage. Illustration by L.J.V. Compagno.

present and large, extending over anterior two-thirds of clasper glans, formed as a flat, convex-edged blade with posterior end below apex of exorhipidion. Cover rhipidion greatly reduced, formed as a low lobe above anterior end of rhipidion, pseudosiphon short, narrow, slitlike, extending opposite most of the base of the cover rhipidion but not reaching exorhipidion. Apopyle and hypopyle connected by a long clasper groove, with its dorsal margins not fused in the specimens examined. Clasper siphons long and narrow, extending anterior to pelvic-fin bases about 0.9 of pectoral-pelvic space and nearly reaching pectoral-fin bases.

Clasper skeleton with almost all elements present. Axial cartilage or appendix-stem connected proximally by a single, very short basal segment (B1) to pelvic basipterygium, but with no apparent beta cartilage. Clasper shaft, formed from axial cartilage and tightly rolled dorsal and ventral marginal cartilages, moderately slender, forms a flattened cylinder extending to clasper glans. Clasper glans skeleton comprises a large, narrow, curved, hooked, spear-tipped dorsal terminal and more distally expanded ventral terminal with enlarged clasper denticles strongly anchored to its tip, articulating with and separated along their proximomesial third to short, narrow, cylindrical end-style (terminal extension of axial cartilage); elongated, mesially twisted posterior ends of terminal cartilages separated by a narrow gap. Accessory dorsal marginal cartilage (RD2) is a long, wedge-shaped, distally tapering cartilage that supports the weak cover rhipidion. Accessory dorsal terminal cartilage (TD2) is a small, elongated, blade-like, distally expanded cartilage that extends along anterior end of clasper glans from dorsal marginal nearly to tip of abbreviated end-style, supports rhipidion. Accessory ventral terminal cartilages (TV2 and TV3) support exorhipidion, consist of a posteriorly tapering, thick TV3 cartilage that articulates anteriorly with a lateral projection of the TV, and an elongated, subrectangular TV2 cartilage that articulates with anterolateral end of TV3, extends anteriorly to barely reach the distal end of the ventral marginal. A short, broad, wedge–like accessory terminal cartilage (T3) opposite the TD2 cartilage is proximally sheathed by terminal extension of ventral marginal. T3 cartilage ends well anterior to TV3-TV articulation.

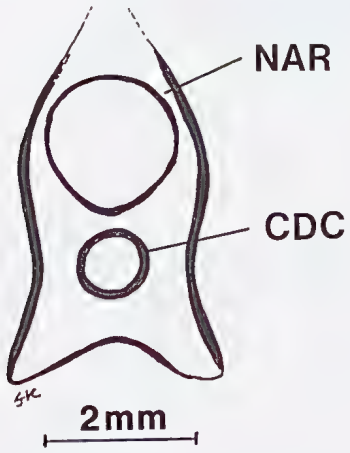

Fig.8. *Galeus gracilis*, vertebral calcification pattern, CSIRO CA4478, 333 mm TL adult male paratype. Abbreviations: CDC – calcified double cone; NAR – neural arch. Illustration by L.J.V. Compagno.

First dorsal fin low, narrow at apex and not falcate, with slightly undulating or convex anterior margin, bluntly angular apex, slightly convex posterior margin, abruptly angular free rear tip, and slightly concave inner margin. First dorsal-fin origin about opposite midbases of pelvic fins, midpoint of dorsal-fin base about opposite pelvic-fin insertions, insertion about equidistant between anal-fin origin and pelvic-fin insertions or 1.5 times closer to pelvic fins, free rear tip about inner margin length anterior to anal-fin origin. Posterior margin nearly vertical, insertion well anterior to dorsal apex. First dorsal-fin base 1.7-2.3 in interdorsal space, 3.3-4.5 in dorsal caudal-fin margin; first dorsal-fin height 1.1-2.0 in first dorsal-fin base; first dorsal-fin inner margin 1.4-2.3 in first dorsal-fin height, 2.4-3.0 in first dorsal-fin base.

Second dorsal fin low, narrow at apex and not falcate, about 0.9 of first dorsal-fin area, second dorsal-fin height 0.7-0.9 of first dorsal-fin height, base 0.7-1.0 of first dorsal-fin base. Second dorsal fin with nearly straight anterior margin, bluntly angular apex, straight posterior margin, broadly angular free rear tip, nearly straight or slightly convex inner margin. Second dorsal-fin origin about opposite last third of anal-fin base, insertion slightly in front to slightly behind anal-fin free rear tip, free rear tip above or just in front of upper caudal-fin origin. Posterior margin slanting posteroventrally from apex, insertion well anterior to dorsal apex. Second dorsal-fin base 0.5-0.7 in dorsocaudal space, second dorsal-fin height 1.5-1.7 in second dorsal-fin base, second dorsal-fin inner margin 1.4-1.6 in second dorsal-fin height and 2.3-2.5 in second dorsal-fin base.

Anal fin low, narrow at apex, not falcate, and at least twice the area of second dorsal fin, anal-fin height 0.8-1.0 in second dorsal-fin height and base 1.9-2.1 times second dorsal-fin base. Anal-fin anterior margin nearly straight or slightly undulated, apex rounded, posterior margin slightly concave, free rear tip acutely pointed, and inner margin straight. Anal-fin base without preanal ridges, anal-fin origin 0.7-0.9 of its base length behind pelvic-fin insertions, free rear tip 3.0-3.6 times anal-fin inner margin anterior to lower caudal-fin origin. Anal-fin posterior margin slanting posterodorsally, anal-fin insertion far behind apex. Anal-fin base 0.5-0.7 in anal-caudal space, anal-fin height 3.0-3.7 in anal-fin base, anal-fin inner margin 1.8-2.0 in anal-fin height and 5.5-7.4 in anal-fin base.

Caudal fin very narrow-lobed and asymmetrical, with large terminal lobe and ventral lobe hardly developed. Caudal fin elongated, dorsal margin 2.6-3.0 in precaudal length. Preventral caudal-fin margin 2.7-3.3 in dorsal caudal-fin margin, terminal lobe 4.7-4.8 in dorsal caudal-fin margin, subterminal margin 0.8-1.1 in terminal margin. Dorsal caudal-fin margin slightly undulated above, without lateral undulations, preventral margin basally concave and apically straight, tip of ventral

caudal-fin lobe broadly angular, upper and lower postventral margins not differentiated, postventral margin broadly concave, subterminal notch a narrow, deep slot, subterminal margin nearly straight, terminal margin straight to convex, lobe formed by these margins angular, and tip of tail angular.

Total vertebral counts (TC) 130-134, monospondylous precaudal (MP) centra 33-36, diplospondylous precaudal (DP) centra 41-43, precaudal (PC) centra 74-78, and diplospondylous caudal (DC) centra 55-56. MP counts 26.1-26.8%, DP counts 31.3-31.5%, and DC counts 41.7-42.3% of TC counts. Ratios of DP/MP counts 1.2, DC/MP counts 1.6, 'A' ratio 133-146, 'B' ratio 86-133 (see Table 2 for detailed count data and ratios). Transition between MP and DP centra well behind pelvic origins and over rear ends of pelvic bases, about 5 or 6 centra

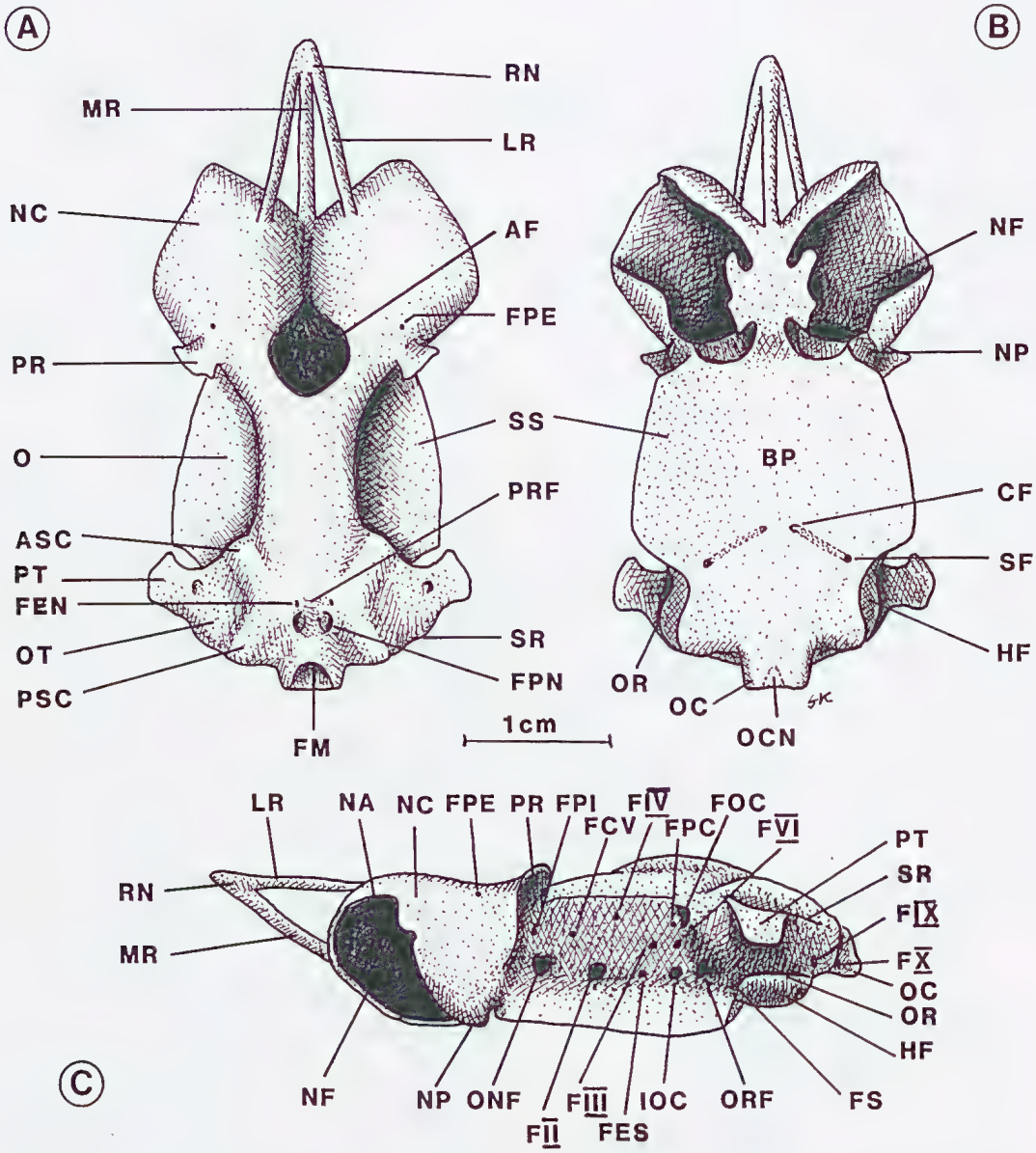

Fig.9. *Galeus gracilis*, chondrocranium from CSIRO CA4478, 333 mm TL adult male paratype. A, dorsal; B, ventral; C, lateral views. Abbreviations: AF – anterior fontanelle; ASC – anterior semicircular canal; BP – basal plate; CF – internal carotid foramen; FCV – foramen for anterior cerebral vein; FEN – endolymphatic foramen; FES – foramen for efferent spiracular artery; FM – foramen magnum; FOC – foramen for superficial opthalmic nerve; FPC, FPE and FPI – cranial, external and orbital foramina of deep ophthalmic nerve; FPN – perilymphatic foramen; FII – optic nerve foramen; FIII – oculomotor nerve foramen; FIV – trochlear nerve foramen; FVI – abducens nerve foramen; FIX – glossopharyngeal nerve foramen; FX – vagus nerve foramen; HF – hyomandibular facet; IOC – interorbital canal; LR – lateral rostral cartilage; MR – medial rostral cartilage; NA – nasal aperture; NF – nasal fontanelle; NC – nasal capsule; NP – orbital notch; O – orbit; OC – occipital condyle; OCN – occipital centrum; ONF – orbitonasal foramen; OR – opisthotic ridge; ORF – orbital fissure; OT – otic capsule; PR – preorbital process; PRF – parietal fossa; PSC – posterior semicircular canal; PT – postorbital process; RN – rostral node; SF – stapedial foramen; SR – sphenopterotic ridge; SS – suborbital shelf. Illustration by L.J.V. Compagno.

behind pelvic girdle. Last few MP centra before MP-DP transition moderately enlarged, not forming a 'stutter zone' of alternating long and short centra. Diagonal calcifications absent from vertebral centra; intermedialia very weakly calcified and hardly indented medially.

Intestinal valve of conicospiral type, 2 specimens counted with 6 and 7 turns.

Chondrocranium (Fig.9) with elongated, slender, cylindrical rostral cartilages, these not hypercalcified and united at their distal tips into a short, unfenestrated rostral node. Medial rostral cartilage approximately 39% of NBL, distance between bases of lateral rostral cartilages 2.5 in medial rostral cartilage. Nasal capsules large, high, diagonally oval, slightly longer than wide, width across them 71% of NBL, length of capsule 0.9 in its width. Anterior margins of nasal capsules nearly straight, slanted obliquely at approximately a right angle to each other. Nasal apertures large, on anterolateral faces of capsules, separated from large nasal fontanelles by a broad channel. Ectethmoid chambers inside nasal cavities, at posterior edges of nasal fontanelles and not visible ventrally. Subnasal plate in the form of narrow medial extensions of the lateral capsule wall, butterfly wing-shaped lateral extensions of the narrow, high internasal septum bordering the nasal fontanelles. Prominent groove or channel on dorsal surface of nasal capsules on midline between anterior fontanelle and base of medial rostral cartilage. Small external profundus nerve foramina on posterodorsal surface of nasal capsules just anterior to bases of preorbital processes. Anterior fontanelle subrhomboidal and small, width about 1.1 times in its length and about 18% of NBL. Dorsal lip of fontanelle flat, without an epiphysial foramen. Cranial roof arched between orbits, well elevated above level of postorbital processes and forming a low flat dome above the posterior half of the orbits. Parietal fossa small, narrow, and moderately deep. Orbital notches relatively deep. Basal plate flat from orbital notches to occipital centrum, without keels. Internal carotid foramina about one-third as far from each other than from the stapedial foramina on either side of them. Supraorbital crests absent, with a low angular ridge connecting the bases of the preorbital and postorbital processes. Preorbital processes low, prominent, trapezoidal, laterally expanded, and obliquely elevated almost to dorsalmost dome of cranial roof. Postorbital processes broad-based, flat, angled anteriorly in dorsal view and ventrally in lateral view; distal blade of processes slightly expanded, with broadly convex lateral edge. Small foramen present at base of each postorbital process. Width across preorbital processes 55% of NBL, width across postorbital processes 66% of NBL. Orbits horizontally subrectangular in lateral view, with contents indicated in Figure 9C. Weak ledge between suborbital shelves and nasal capsules. Suborbital shelves arcuate-angular in shape, with edges deflected ventrally in lateral view and diverging posteriorly in dorsoventral view; shelves not expanded laterally to distal ends of the postorbital processes in dorsal view. Suborbital shelves relatively narrow, width across them 63% of NBL. Otic capsules not greatly expanded or inflated, their lengths about 30% of NBL and greatest width across them 48% of NBL. Sphenopterotic ridges low, posteriorly convergent, without pterotic horns. Opisthotic ridges low, not extending laterally to edges of sphenopterotic ridges. Hyomandibular facets small, horizontally oval, extending across middle third of otic capsules, not exserted posteriorly. Occipital condyles narrow, prominently exserted from occiput, with a single occipital centrum between them.

Colour in alcohol light gray-brown above, lighter below, back and upper surface of pectoral fin darker, anal fin, subterminal caudal web and terminal caudal-fin lobe dusky but with light margins, bases and proximal webs of dorsal fins dark but with light posterior margins. Bold dark gray-brown saddle-marks on base of precaudal tail below first dorsal-fin base, below second dorsal-fin base, at dorsal base of caudal fin just behind origin, and as a vertical band anterior to subterminal notch of caudal fin and delimiting the light terminal caudal-fin lobe. No dark blotch on hypaxial caudal-fin lobe. Saddle marks without light margins. In some specimens a broad, poorly defined dark blotch extends on sides and back from over pectoral fins to just in front of pelvic-fin bases. No small dark or light spots on fins or body. Inside of mouth dark gray or blackish.

Weight of H1208.01 (335 mm female holotype) is 116 gm; 2 adult male paratypes weigh 79 gm (CA4477, 329 mm) and 70 gm (CA4478, 333 mm).

Mode of reproduction. Unknown.

Distribution. At present *Galeus gracilis* is known from the northwestern continental slope off Western Australia and the Northern Territory (Fig.10), on the bottom at depths from 290 to 453 m.

Bessednov (1969) recorded two specimens of *Galeus eastmani* from the Gulf of Tonkin off Vietnam at 40 m depth. Springer (1979) and Compagno (1984, 1988) accepted this record, but Bessednov's *Galeus* may be closer to *G. gracilis* than *G. eastmani*. The specimen illustrated, a 331 mm female (Bessednov's, fig. 11; also included here as Fig.11), agrees with *G. gracilis* in its longer preorbital snout, smaller eye, and more boldly marked saddles, but agrees with *G. eastmani* as described by Nakaya (1976) in having dark blotches on the hypaxial and terminal caudal fin lobes (absent in *G. gracilis*). We consider the assignment of Bessednov's specimens to *G. eastmani* as questionable pending their reexamination.

Comparison with Other Species

The traditional external morphology and morphometrics, colouration and vertebral counts used in Springer's (1979) review of the genus *Galeus* has been supplemented by the work of Nakaya (1976), Muñoz-Chapuli & Ortega (1985), Tachikawa & Taniuchi (1987),

and Compagno (1988). The morphological character systems they demonstrated to elucidate the systematics and interrelationships of the genus include: the detailed external morphology and anatomy of the claspers; the chondrocranial morphology; the denticle and dental morphology as revealed by the scanning electron microscope; the morphology of the pectoral fin skeleton. While such work points to the feasibility of elucidating the cladistic relationships of *Galeus*, several species are at present incompletely known in crucial character systems, particularly the chondrocranium, claspers and pectoral fin skeleton. There are linked problems with the monophyly and composition of *Galeus*, with its interrelationships with other galeine genera, and with lack of knowledge of some character systems in other galeines (see Compagno, 1988). This would make a cladistic

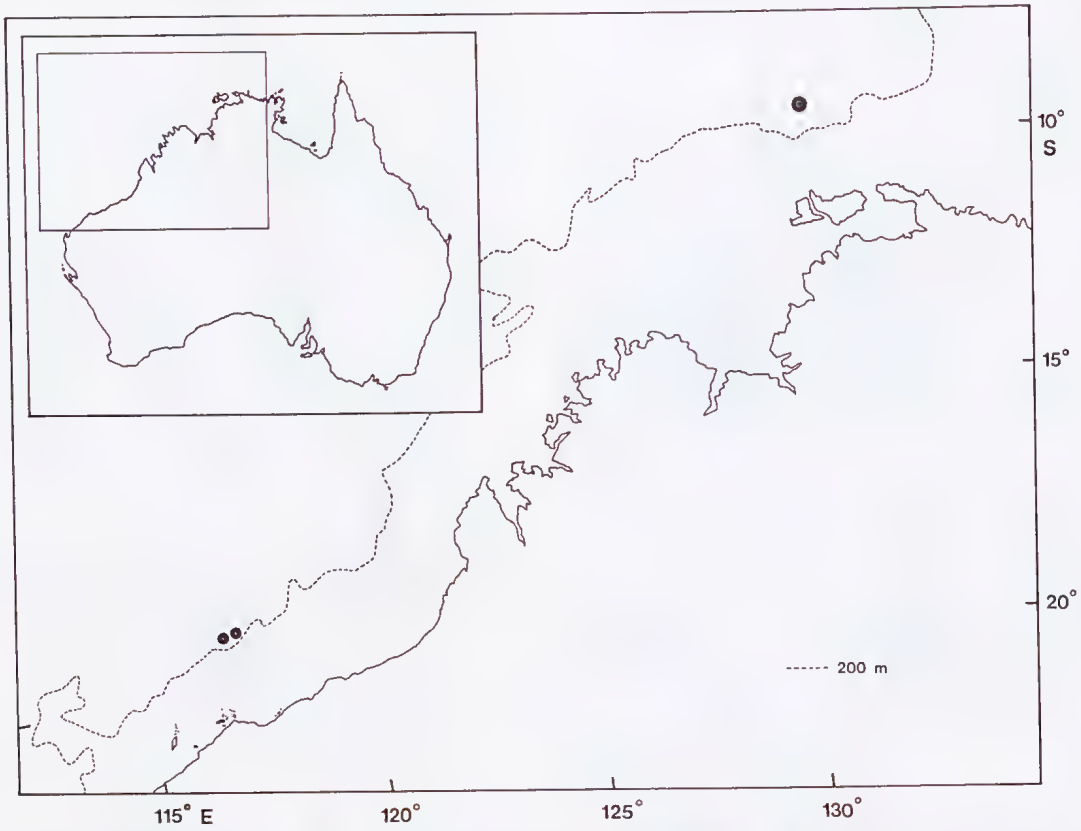

Fig.10. *Galeus gracilis*, distribution map. Inset: Australian continent with known range on North West Shelf circumscribed by square. Main map: enlargement of inset square with records of type specimens shown as black dots. Map by P. White.

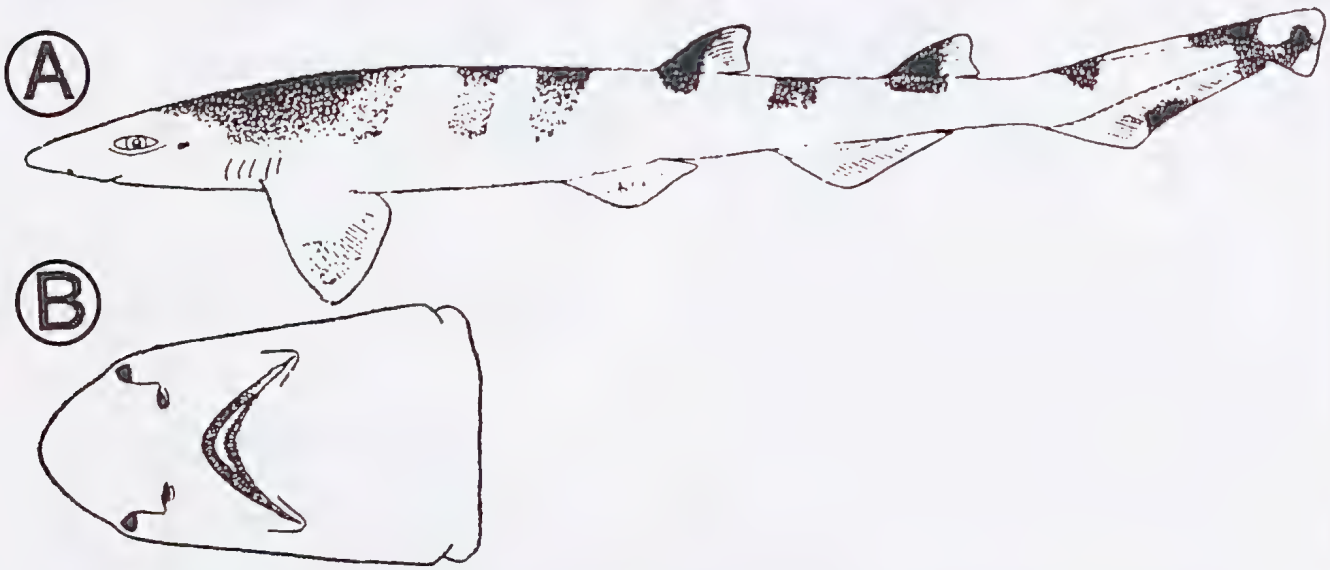

Fig.11. '*Galeus eastmani*' from the Gulf of Tonkin, Vietnam. A, lateral view of a 331 mm TL female; B, underside of head, enlarged. From Bessednov (1969).

analysis of *Galeus* premature.

For the descriptive purposes of this paper, other species of *Galeus* are compared and contrasted with *G. gracilis* without attempting a cladistic analysis. *Galeus gracilis* may be closest to *Galeus eastmani*, *G. longirostris*, and *G. nipponensis* from Japan; all four species have a relatively slender body, long precaudal tail, caudal peduncle not greatly compressed, and a relatively small anal fin. *Galeus gracilis* appears to be more distant from *G. sauteri* and *G. schultzi* from the western North Pacific and is not close to the *Asymbolus*-like *G. boardmani* from Australia (see Compagno 1988). *Galeus gracilis* is not close to eastern Pacific or Atlantic members of *Galeus*.

Galeus eastmani. *Galeus gracilis* most closely resembles the small *G. eastmani* in general morphology, size (adult *eastmani* to 395 mm TL) and in its similar tooth row, MP vertebral, and intestinal valve counts. *Galeus eastmani* as characterised from the study material and Nakaya's (1976) detailed account differs from *G. gracilis* in having a slightly shorter snout (POR 5.8-6.6% TL versus 6.4-7.8% TL for *G. gracilis*); more laterally situated, larger eyes in adults (EYL 3.5-4.2% TL versus 3.2-3.3% TL); possibly shorter anal-caudal space (ACS 0.2 of ANB versus 0.5-0.7); more strongly twisted, bent, bluntly pointed clasper tips (Fig.12A-B); a larger, more angular exorhipidion; a shorter clasper glans (0.4 of distance from apopyle to clasper tip versus 0.6 in *G. gracilis*); a vestigial cover rhipidion (well developed in *G. gracilis*); pseudosiphon absent; a slightly larger pectoral fin (P1A 10.6-13.4% TL versus 9.7-11.0); three fused proximal mesopterygial radial segments (2 in *G. gracilis*); a longer anal fin (ANB 12.6-15.2% TL versus 10.5-11.5); a less bold colour pattern of obscure saddles, but with dark markings on the hypural and terminal caudal fin lobes (absent in *G. gracilis*); more diplospondylous precaudal vertebrae (49-50 versus 41-44).

The chondrocranium of *G. eastmani* (Fig.13D) differs from that of *G. gracilis* in having much shorter rostral cartilages; a broader rostral node; more widely spaced bases on its medial rostral cartilages (distance between bases 1.4 times anterior fontanelle width versus 0.9 in *G. gracilis*); broader nasal capsules (width across capsules 1.4 *x* width across postorbital processes versus 1.0); a broader anterior fontanelle; parallel rather than posteriorly divergent edges on its suborbital shelves; lower postorbital processes; possibly lower occipital condyles.

Galeus boardmani. The little-known *Galeus boardmani* is the only other *Galeus* or *Galeus*-like galeine known from Australia. It resembles *G. gracilis* in its slender proportions, small fins, and dorsolateral eyes, but is otherwise quite distinct. It is compared in detail with *G. gracilis* here.

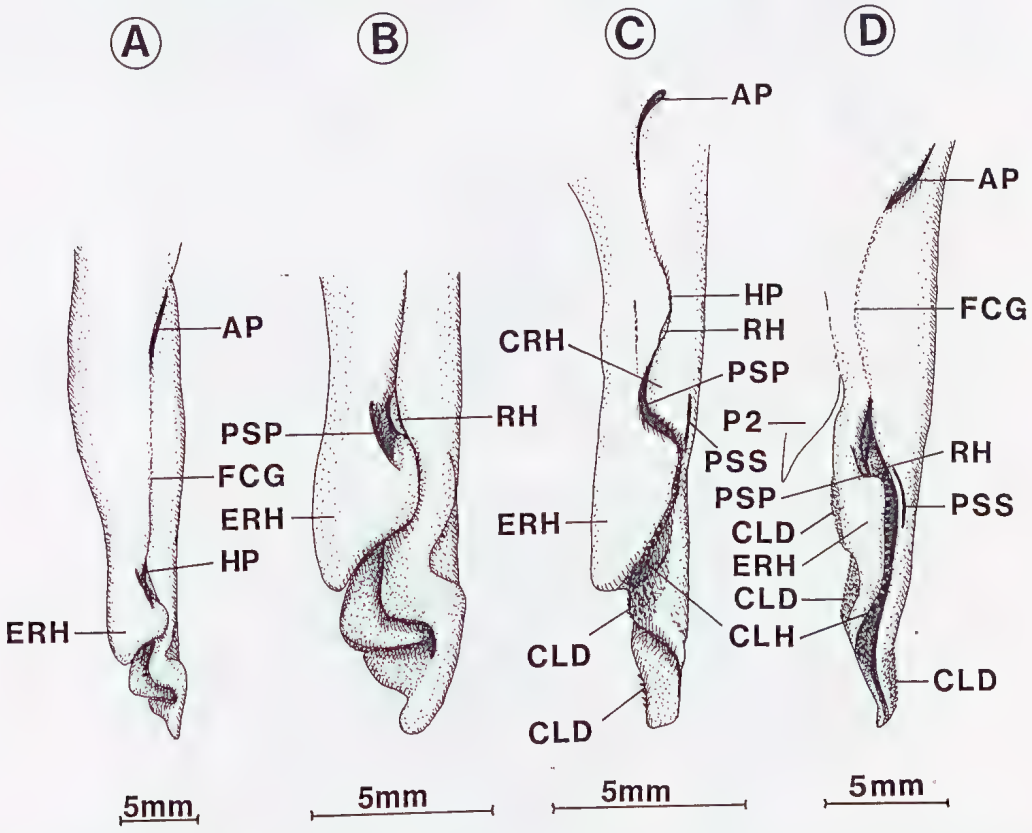

Fig.12. Left claspers of adult males of three species of *Galeus* in dorsal view. A-B, *Galeus eastmani*, SU-35469, 344 mm TL. A, entire clasper; B, enlarged view of clasper glans; C, *Galeus arae*, SB 2420, 305 mm TL, entire clasper; D, *Galeus polli*, RV *Africana* A6948 059 E17, 326 mm TL, entire clasper. Scale bars = 5 mm. Abbreviations as in Figure 6, except for CLH – clasper hooks (on medial edge of exorhipidion); FCG – fused clasper groove.

Galeus boardmani is provisionally assigned to *Galeus* but may be closer to members of the genus *Asymbolus* (Compagno, 1988). As characterised from specimens and from Whitley's (1928, 1940) accounts, *G. boardmani* grows much larger (adults to 610 mm TL) and has a broader, blunter, shorter snout (POR 0.8 of MOW versus 0.9-1.0 in *G. gracilis*); more elongated anterior nasal flaps and larger posterior nasal flaps; larger eyes in adults (EYL 4.3% TL and 4.0 in HDL versus 3.2-3.3% TL and 5.7-6.7% TL); more tooth rows in adults (67/74 versus 54-57/54-62); possibly a longer precaudal tail (distance from front of vent to dorsal caudal-fin origin approximately 37% TL versus 30.4-35.6% TL); pelvic-fin inner margins partly united as a low 'apron' of skin over claspers in adult males; a more erect first dorsal fin, with a less oblique anterior margin; possibly a longer interdorsal space (1.5 times the anal-fin base versus 1.1-1.2); a long, low ridge the underside of the caudal peduncle, and a row of enlarged, sawlike denticles on the ridge and the preventral caudal-fin margin (absent in *G. gracilis*); a shorter caudal fin (DCM in adults about 22% TL versus 25.4-27.9% TL); more numerous dark saddle markings (12-13 versus about 4) with conspicuous light edges (absent in *G. gracilis*); a light mouth (dark in *G. gracilis*); more numerous vertebrae, including DP counts (58 versus 41-43), PC counts (95 versus 74-78), and total counts (148 versus 130-134); more numerous intestinal valve turns (11 versus 6-7).

The claspers of *G. boardmani* and *G. gracilis* are somewhat similar in being relatively short, thick at the base, and gradually tapering, but there are numerous differences: those of *G. boardmani* are shorter (6.9% TL versus 10.3-10.8% TL) and have a shorter glans (Fig.14) about 0.5 of the distance from the apopyle to clasper tip (0.6 in *G. gracilis*); a well-developed clasper envelope (vestigial or absent in *G. gracilis*); a small, low bilobate

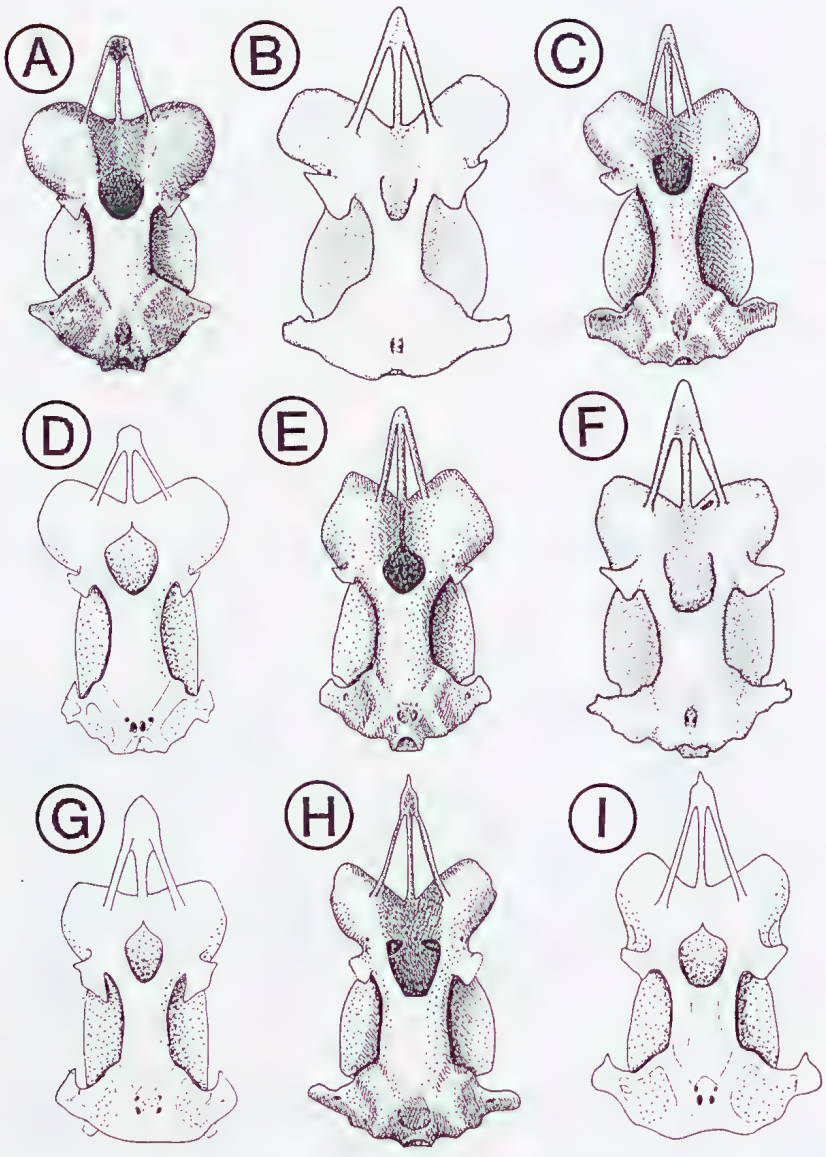

Fig.13. Chondrocrania from nine species of *Galeus* in dorsal view, adjusted to same nasobasal length (NBL). A, *G. arae*; B, *G. atlanticus*; C, *G. boardmani*; D, *G. eastmani*; E, *G. gracilis*; F, *G. melastomus*; G, *G. nipponensis*; H, *G. polli*; I, *G. sauteri*. A,C,E,H – illustrations by L.J.V. Compagno. A – modified from Compagno (1988); B,F – from Munoz-Chapuli & Ortega, 1985; D,G,I – modified from Nakaya (1976).

exorhipidion without a free posterior end (enlarged and bulbous, and with a free posterior end in *G. gracilis*); no enlarged anteriorly directed denticles on the exorhipidion, mesial, and lateral tips of the claspers (present in *G. gracilis*); a larger cover rhipidion that partly conceals the rhipidion; clasper tips not twisted (moderately twisted in *G. gracilis*).

The clasper skeletons of *G. boardmani* and *G. gracilis* have a full complement of clasper cartilages except for the beta cartilage, but differ markedly in the morphology of these cartilages. *Galeus boardmani* has broader dorsal and ventral marginals (Fig.15); a broader, less tapering axial cartilage; a longer appendix-stem over half the length of the ventral terminal cartilage; much smaller ventral terminal 2 and 3 cartilages (TV2 and TV3), reflecting its small exorhipidion; a larger, more hooked accessory terminal cartilage (T3; wedge-shaped in *G. gracilis*); a broader dorsal terminal 2 (TD2) cartilage; a smaller, more truncated accessory dorsal marginal (RD2) cartilage; the dorsal terminal cartilage much shorter and smaller than the ventral terminal cartilage (equal-sized and equally long in *G. gracilis*); the dorsal and ventral terminals without twisted tips (present in *G. gracilis*).

The chondrocranium of *G. boardmani* (Figs 13C,15) is generally similar to that of *G. gracilis* but differs in having shorter nasal capsules; smaller nasal fenestrae; narrower-based, broader lateral extensions of the internasal plate; a more U-shaped anterior fontanelle; a narrower cranial roof with the section anterior to the optic nerve foramen flat (arched above the orbits in *G. gracilis*); higher, larger orbits; larger, more dorsally elevated preorbital processes; broader, more posteriorly divergent and convex suborbital shelves; more laterally directed postorbital processes; shorter, higher hyomandibular facets; lower occipital condyles.

***Galeus longirostris* and *G. nipponensis*.** The two Japanese species *G. longirostris* and *G. nipponensis* as characterised by Nakaya (1976), Springer (1979) and Tachikawa & Taniuchi (1987) are similar to *G. gracilis* in their relatively long prenarial snouts (PRN 0.9-1.5 times EYL), dorsolateral eyes, long abdomens (PPS 12.7-16.5% TL), short anal fins (ANB less than 13% TL), and a long interdorsal space relative to the anal-fin base (IDS 1.0-1.5 times ANB). These species differ from *G. gracilis* in attaining a much greater size at maturity (adults 660-803 mm TL in *G. longirostris* and 530-656 mm TL in *G. nipponensis*) and in having much longer claspers (CLO at least 11.0% TL versus 10.3-10.8% TL in *G. gracilis*) that extend behind the anal-fin origin (not reaching it in *G. gracilis*); cylindrical shafts and broad, strongly twisted tips on the claspers; clasper glans less than 0.5 of distance from apopyle to clasper tip (0.6 in *G. gracilis*); a vestigial cover rhipidion; darker dorsal colouration, with saddle markings irregular or absent in adults; white to gray-white mouths (blackish in *G. gracilis*); more MP centra (MP 37-40 in *G. nipponensis*, 40-45 in *G. longirostris* versus 33-36).

Galeus longirostris additionally differs from *G. gracilis* in its longer snout (POR 7.9-8.3% TL versus 6.4-7.8% TL); more broadly rounded snout tip; slightly larger eyes

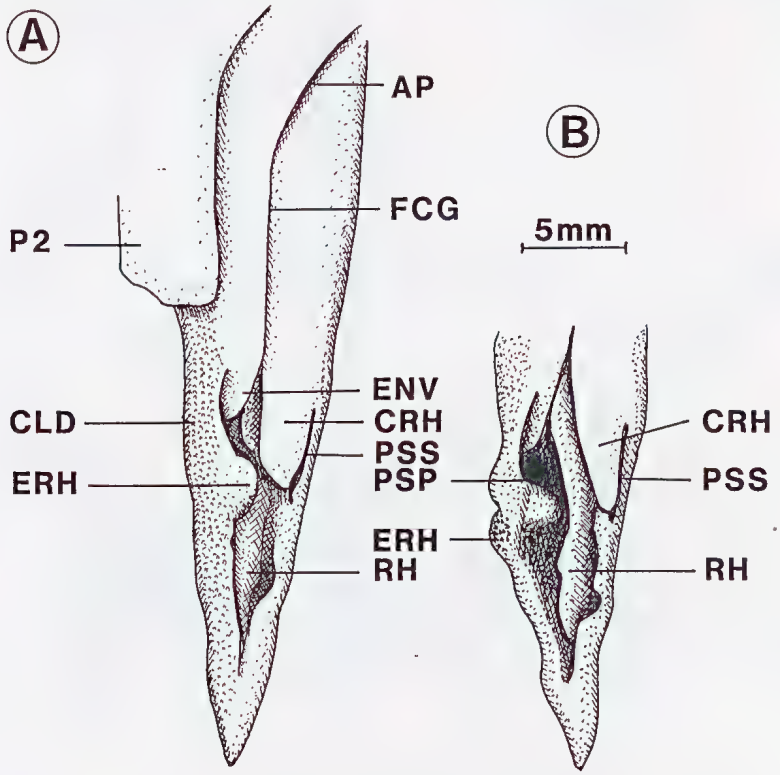

Fig.14. *Galeus boardmani*, left clasper in dorsal view from CSIRO H989.04, 432 mm adult male. A, glans not dilated; B, glans spread. Abbreviations as in Figure 6, except for FCG – fused clasper groove. Illustration by L.J.V. Compagno.

in adults (EYL 3.4-4.0% TL versus 3.2-3.3% TL); more broadly arched mouth; slightly longer labial furrows (2.1-2.5% TL versus 1.6-2.1% TL); slightly shorter caudal peduncle (ACS/ANB ratio 0.3-0.5 versus 0.5-0.7); larger pectoral fins (P1A 11.2-12.6% TL versus 9.7-11.0% TL); more numerous PC vertebral counts (91-97 versus 74-78).

Galeus nipponensis additionally differs from *G. gracilis* in its higher pectoral-fin radial counts (19 versus 16) and three fused proximal radials on the mesopterygium (2 in *G. gracilis*).

All three species have enlarged, anteriorly directed groups of denticles on the mesial and lateral faces of the clasper tip, but they are more prominent and numerous in *G. gracilis* than in *G. nipponensis*, but less numerous than in *G. longirostris*.

The chondrocranium of *G. longirostris* was not available for study, but that of *G. nipponensis* (Fig.13G) differs from that of *G. gracilis* in having thicker rostral cartilages; more widely spaced bases on the lateral rostral cartilages (distance between bases 1.7 times the anterior fontanelle width in *G. nipponensis*, 0.9 in *G. gracilis*); a much larger rostral node; smaller nasal capsules with nearly transverse anterior edges (strongly oblique in *G. gracilis*); larger postorbital processes; a more longitudinally oval anterior fontanelle; parallel edges to the suborbital shelves; stronger anterior projections on the postorbital processes; possibly more posteriorly exserted hyomandibular facets; possibly lower occipital condyles.

***Galeus sauteri* and *G. schultzi*.** *Galeus sauteri* from Taiwan and possibly the Philippines, and *G. schultzi* from the Philippines are less similar to *G. gracilis* than other western North Pacific *Galeus*. They are characterised here from specimens and from the accounts of Nakaya (1967), Springer (1979), and Compagno (1984, 1988). *Galeus sauteri* and *G. schultzi* agree with *G. gracilis* in having a relatively long abdomen (PPS 11.5-14.5% TL versus 14.3-16.0% TL); low vertebral counts (see Table 2); relatively small size. *Galeus gracilis* may lie between *G. schultzi* (adults 254-297 mm TL) and *G. sauteri* (adults 354-450 mm TL). Both species differ from *G. gracilis* in their shorter prenarial snouts (PRN 0.6-0.8 of EYL versus 0.9-1.3); less pointed, more bluntly rounded snouts; stouter bodies; shorter, more compressed caudal peduncles (ACS/ANB ratio 0.2-0.3 versus 0.5-0.7); clasper tips reaching behind the anal-fin origin;

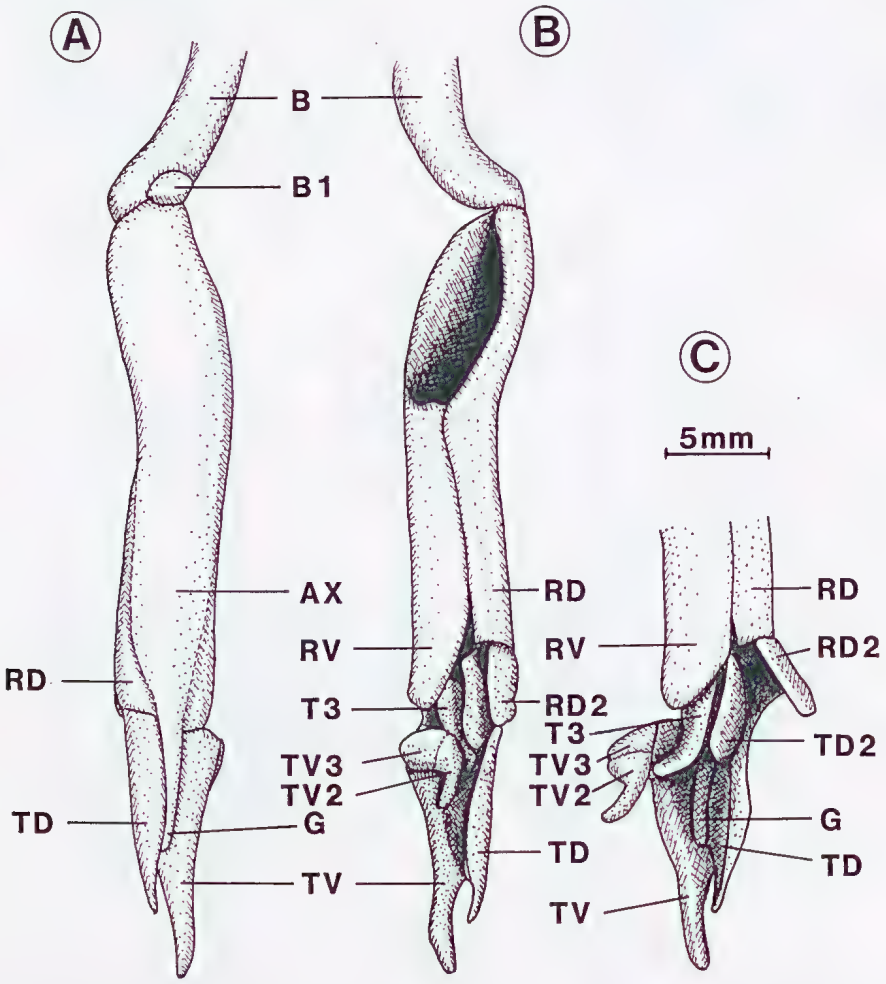

Fig.15. *Galeus boardmani*, clasper skeleton, CSIRO H989.04, 432 mm adult male. A, ventral view; B, dorsal view, terminal cartilages not dilated; C, dorsal view of glans, terminal cartilages spread. Abbreviations as in Figure 7. Illustration by L.J.V. Compagno.

somewhat larger pectoral fins (P1A 10.6-13.4% TL in *G. sauteri* and 12.3-12.6% TL in *G. schultzi* versus 9.7-11.0% TL); longer anal-fin base (12.6-16.9% TL in *G. sauteri* and over 13% TL in *G. schultzi*); poorly-developed saddles on the body and precaudal tail; dark markings on the hypural and terminal caudal-fin lobes (lacking in *G. gracilis*).

Galeus schultzi additionally differs from *G. gracilis* in its shorter preoral snout (5.4-5.9% TL versus 6.4-7.8% TL); smaller mouth (MOW 6.5-6.7% TL versus 7.0-8.1% TL); the long preanal ridge on the anal fin, bringing the anal-fin origin almost to the pelvic-fin insertions (absent in *G. gracilis*); shorter labial furrows (ULA about 0.7% TL versus 1.6-2.1% TL); possibly fewer tooth rows (48/less than 48 versus 54-57/54-62); possibly more elongated claspers, according to Springer (1979).

Galeus sauteri also differs from *G. gracilis* in having laterally situated eyes and reduced subocular ridges; more numerous tooth rows (70-78/82 versus 54-57/54-62); shorter claspers (CLO 7.3% TL versus 10.3-10.8% TL); hourglass-shaped claspers, with a broad base, narrow midshaft and expanded glans (Compagno, 1988, fig.13.20D; tapered in *G. gracilis*); broad, strongly twisted clasper tip; vestigial cover rhipidion (well developed in *G. gracilis*); prominent black blotches on the dorsal fins (dusky markings in *G. gracilis*); gray mouth (dark grey or black in *G. gracilis*); slightly more numerous intestinal valves (8-9, mean 8.7 in 6 *G. sauteri* versus 6-7).

The chondrocranium of *G. sauteri* (Fig.13I) differs from that of *G. gracilis* in having more widely spaced bases on the lateral rostral cartilages (distance between bases 1.5 times anterior fontanelle width in *G. sauteri*, about 0.9 in *G. gracilis*); smaller, more widely spaced nasal capsules; a broader anterior fontanelle and cranial roof; larger preorbital processes; larger otic capsules; possibly lower occipital condyles.

***Galeus arae* complex and *G. piperatus*.** The western North Atlantic *Galeus arae* and *G. piperatus* from the

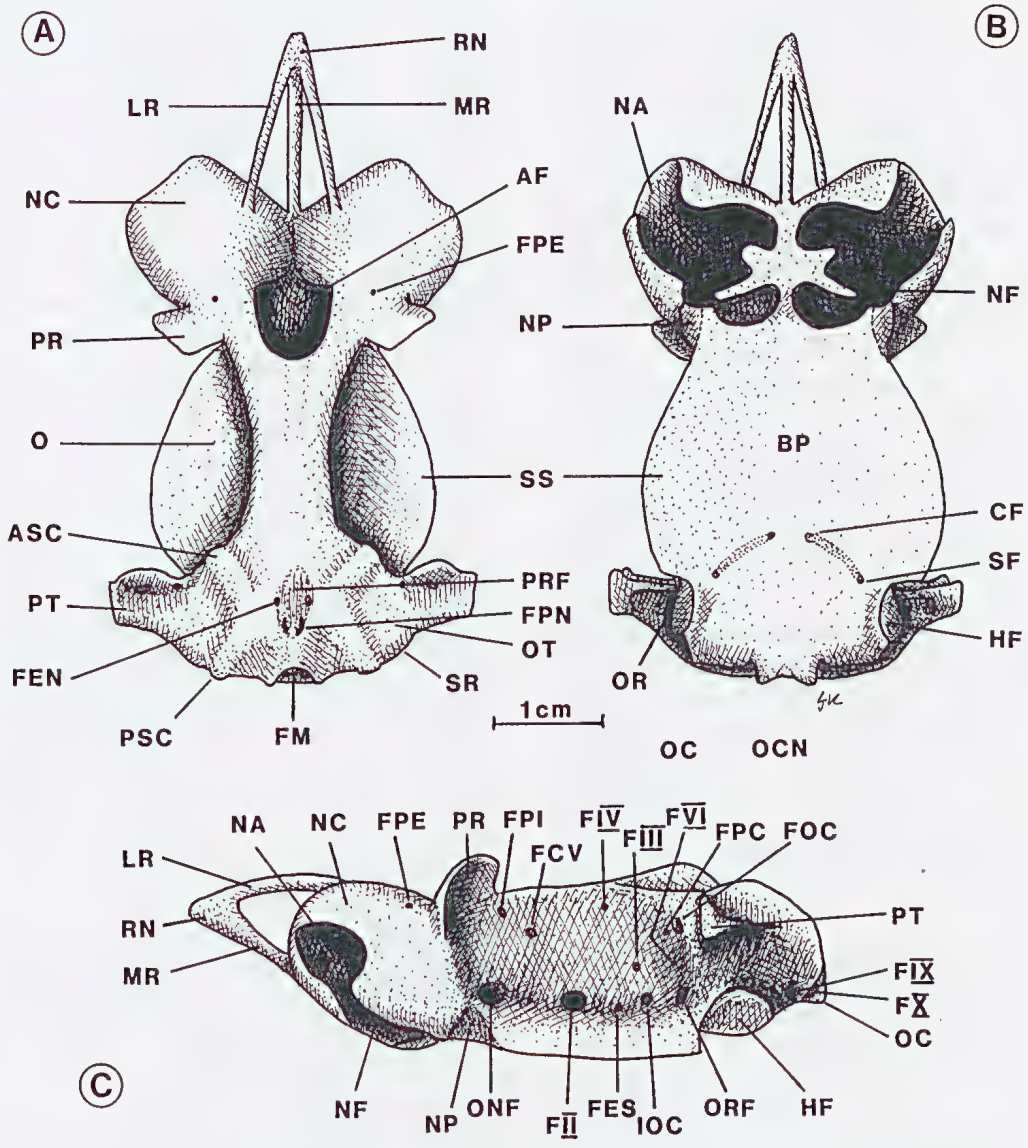

Fig.16. *Galeus boardmani*, chondrocranium from CSIRO H989.04, 432 mm adult male. A, dorsal view; B, ventral view; C, lateral view. Abbreviations as in Figure 9. Illustration by L.J.V. Compagno.

Gulf of California are very close, but certain aspects of the morphology of the latter are not well known. Additionally, *G. arae* was subdivided by Springer (1979) into three allopatric subspecies of uncertain status: the typical *G. arae arae* of the continental slopes from South Carolina south to Costa Rica; *G. a. antillensis* Springer, 1979, a Caribbean island form from the Straits of Florida to Cuba, Hispanola, Puerto Rico, and the Leeward Islands; *G. a. cadenati* Springer, 1966, from the continental slope off Panama and Colombia. Muñoz-Chapuli & Ortega (1985) suggested that Springer's arrangement was problematical because of differences in mode of reproduction between *G. a. antillensis* (possibly oviparous) and *G. a. arae* (ovoviviparous), and that this difference "would seem to be a specific character". *Galeus a. antillensis* and *G. a. cadenati* apparently attain a larger size than typical *G. a. arae*, and the little-known *G. a. cadenati* has a consistently longer anal-fin base and shorter anal-caudal and pelvic-anal spaces than the other two subspecies. For purposes of comparison with *G. gracilis*, the subspecies of *G. arae* are mostly considered together, although they may represent a complex with three separate species plus *G. piperatus* in a superspecies. Springer (1966) had originally described *G. a. cadenati* as a full species, but later (Springer, 1979) reduced its rank.

Data on *G. arae* are from specimens and Springer (1966, 1979), and on *G. piperatus* from Springer & Wagner (1967) and Hubbs & Taylor (1969). *Galeus arae* and *G. piperatus* agree with *G. gracilis* in being small (adults from 255-360 mm in *G. a. arae*, but up to 435 mm TL in *G. a. antillensis*, and 296-302 mm TL in *G. piperatus*) and in having similar tooth row and monospondylous vertebral counts. These species differ from *G. gracilis* in having a broadly rounded snout tip; larger eyes in adults (3.4-4.3% TL versus 3.2-3.3% TL); stouter bodies; shorter, broader precaudal tails with shorter pelvic-anal spaces (PAS/ANB 0.2-0.5 versus 0.8-1.0); shorter anal-caudal spaces (ACS/ANB 0.1-0.4 versus 0.5-0.7); shorter abdomens in adults (PPS 8.1-13.0% TL versus 14.3-16.0% TL); more cylindrical claspers with an hourglass or bilobate shape (Fig.12C); blunt clasper tips that extend behind the anal-fin origin; slightly larger pectoral fins in adults (P1A 10.5-12.2% TL in *G. arae* and 12.6-13.0% TL in *G. piperatus* versus 9.7-11.0% TL); slightly longer to considerably longer anal-fin bases (10.3-13.6% TL in *G. a. arae*, up to 15.0% TL in *G. a. cadenati* and 12.6-13.0 in *G. piperatus* versus 9.7-11.0% TL); a darker ground colour in adults, with either more numerous blotches and saddles or with no markings.

Galeus piperatus additionally differs from *G. gracilis* in having a slightly broader mouth (MOW 8.3-9.2% TL versus 7.0-8.1% TL) and fewer precaudal centra (66-72 versus 74-78), while *G. arae* differs from *G. gracilis* in having lateral eyes with the subocular ridge reduced (not known for *G. piperatus*). The claspers of *G. piperatus* are poorly known, but those of *G. arae* (Fig.12C) differ from *G. gracilis* in having a slightly longer glans (0.7 of distance from apopyle to clasper tip, versus 0.6); more twisted tips; prominent clasper hooks on the exorhipidion; a larger cover rhipidion; a larger exorhipidion.

The chondrocranium of *G. piperatus* is not known, but that of *G. arae* (*G. a. arae*, Fig.13A, not known in other subspecies) differs from *G. gracilis* in the more widely spaced bases of its lateral rostral cartilages (1.3 times the anterior fontanelle width versus 0.9 times); more laterally expanded nasal capsules (width across them 77% of NBL versus 71% of NBL); smaller, more laterally directed postorbital processes; more convex edges on the suborbital shelves; slightly larger otic capsules.

***Galeus atlanticus* and *G. melastomus*.** *Galeus melastomus* of the eastern North Atlantic has a smaller sympatric relative, *Galeus atlanticus*. These are compared in detail by Muñoz-Chapuli & Ortega (1985), and are characterised here from the account of these authors plus Leigh-Sharpe (1922) and Springer (1979) and from specimens of *G. melastomus*.

Neither of these species is particularly close to *G. gracilis* within *Galeus*, and both differ from it in being larger (adults 480-730+ mm in *G. melastomus* and 384-480 mm in *G. atlanticus*); having larger eyes when adult (over 4% TL versus 3.2-3.3% TL); stouter bodies; shorter precaudal tails with short pelvic-anal spaces (PAS/ANB 0.2-0.4 versus 0.8-1.0) and anal-caudal spaces (ACS/ANB about 0.2 versus 0.5-0.7); shorter abdomens (PAS 8.1-10.2% TL versus 14.3-16.0% TL); larger, broader pectoral fins (greater than 12.0% TL versus 9.7-11.0% TL); more numerous pectoral-fin radials (20-21 in *G. atlanticus* and 22-24 in *G. melastomus* versus 16) and narrower, more axially elongated pectoral-fin skeletons; longer anal-fin bases (greater than 14% TL versus 10.5-11.5% TL); interdorsal space less than the anal-fin base (greater in *G. gracilis*); and more numerous dark saddles and irregular spotting in adults.

Galeus melastomus additionally differs from *G. gracilis* in having lateral eyes with a weak subocular ridge (uncertain in *G. atlanticus*); more numerous tooth rows (69-78/79-84 versus 54-57/54-62); a more compressed caudal peduncle (CPH/CPW 1.9 versus 1.1-1.4); claspers more hourglass-shaped, with blunt, more twisted points; clasper glans shorter (0.4 of distance from apopyle to clasper tip versus 0.6); cover rhipidion vestigial; possibly no pseudosiphon; possibly a more angular exorhipidion; more numerous MP (37-39 versus 33-36) and total (141-151 versus 130) vertebral centra.

The chondrocrania of *G. atlanticus* (Fig.13B) and *G. melastomus* (Fig.13F) differ from that of *G. gracilis* in having more widely spaced bases on their lateral rostral cartilages (distance between bases 1.9 times the anterior fontanelle width in *G. atlanticus*, 1.5 in *G. melastomus* versus 0.9); larger preorbital processes; more posteriorly elongated anterior fontanelles; larger, higher, more laterally directed postorbital processes. That of *G. atlanticus* additionally differs from *G. gracilis* in having more laterally expanded nasal capsules; a narrower cranial roof; broader suborbital shelves; larger otic capsules.

Galeus murinus* and *G. polli. *Galeus murinus* and *Galeus polli* are two eastern North Atlantic species that are not close to *G. gracilis* or to each other. Data on these species is from Cadenat (1959), Springer (1979), Compagno (1984, 1988), Muñoz-Chapuli & Ortega (1985) and specimens. Both agree with *G. gracilis* in their tapered claspers with pointed, moderately twisted clasper tips and in their MP vertebral counts. However, both have larger eyes (greater than 3.5% TL versus 3.2-3.3% TL); stouter bodies; shorter precaudal tails with short pelvic-anal spaces (PAS/ANB 0.2-0.3 versus 0.8-1.0) and anal-caudal spaces (ACS/ANB 0.1-0.2 versus 0.5-0.7); a vestigial cover rhipidion on their claspers; a more angular exorhipidion (more bulbous in *G. gracilis*); interdorsal space less than the anal-fin base (greater in *G. gracilis*); either a uniform dark colouration or a darker ground colour with more dark saddles and irregular spotting in adults.

Galeus murinus has a long abdomen and relatively small pectoral fins, as does *G. gracilis*, but additionally differs in its blunt snout with broadly rounded tip; shorter mouth; presence of a spur on the exorhipidion (Compagno, 1988, fig.13.20B); higher pelvic fins; higher anal fin (ANB/ANH 2.2 versus 3.0-3.7); a crest of enlarged denticles on the preventral caudal-fin margin; fewer PC centra (66-67 versus 74-78); greater size (adults 479-545 mm). *Galeus polli* attains a similar size (adults 255-385 mm TL) to *G. gracilis*, but additionally differs in having lateral eyes, with the subocular ridge reduced; possibly more tooth rows (69/65 versus 54-57/54-62); more compressed caudal peduncle (CPH/CPW 1.6-1.7 versus 1.1-1.4); shorter abdomen (7.8-13.5% TL versus 14.3-16.0% TL); shorter claspers (CLO 5.0-6.3% TL versus 10.3-10.8% TL); clasper hooks on the exorhipidion; more numerous pectoral-fin radials (19 versus 16); a larger anal-fin base (greater than 14% TL versus 10.5-11.5% TL); and more numerous intestinal valve turns (12-14, mean 13.5, sd 0.5, in 16 specimens counted versus 6-7).

The chondrocranium of *G. murinus* has not been studied, but that of *G. polli* (Fig.13H) differs from *G. gracilis* in the more widely spaced bases of its lateral rostral cartilages (1.3 times the anterior fontanelle width versus 0.9 times); smaller, more laterally separated nasal capsules; larger, more posteriorly expanded anterior fontanelle; broader cranial roof; narrower, higher, more laterally directed postorbital processes.

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APPENDIX

Table 1. *Galeus gracilis* n.sp. Proportional dimensions of type specimens as percentages of total length (TL in mm).

Coll. No.	CSIRO H1208-01 Adult female Holotype	CSIRO CA3304 Adult female Paratypes	CSIRO CA4477 Adult male	CSIRO CA4478 Adult male
TL	335	312	329	333
PCL	74.6	71.2	79.0	72.7
PRN	4.2	3.8	4.0	3.0
POR	7.8	6.4	7.3	6.6
POB	7.8	6.7	7.6	6.6
PSP	11.6	10.6	12.2	11.1
PGI	16.1	13.8	16.7	15.3
HDL	22.1	18.3	21.6	19.8
PP1	21.5	19.2	21.3	19.5
PP2	42.1	37.2	40.1	38.4
SVL	44.5	40.7	43.5	42.0
PAL	57.9	54.2	58.4	54.7
PD1	46.6	43.6	44.4	43.2
PD2	65.1	62.8	64.7	60.4
IDS	12.8	12.2	13.4	12.6
DCS	4.2	2.9	3.6	3.6
PPS	15.5	16.0	14.3	15.6
PAS	10.1	8.3	10.3	9.3
ACS	6.3	6.4	7.6	6.0
EYL	3.3	3.2	3.3	3.3
EYH	1.8	1.0	1.2	0.9
INO	6.6	6.4	6.4	6.6
NOW	2.4	2.2	2.4	2.4
INW	3.0	2.6	2.4	2.4
ANF	1.2	0.6	0.6	1.2
SPL	0.9	0.6	0.6	1.2
ESL	0.6	1.0	1.4	0.9
MOL	3.3	3.2	3.8	3.0
MOW	8.1	7.1	7.0	7.8
ULA	1.8	1.6	2.1	1.8
LLA	2.4	1.9	2.1	2.4
GS1	1.8	1.6	1.2	1.5
GS2	1.8	1.6	1.2	1.8
GS3	1.8	1.6	0.9	2.1
GS4	1.8	1.3	1.2	1.8
GS5	2.1	0.6	0.9	1.2
HDH	8.7	6.7	7.0	6.3
HDW	11.6	9.6	9.4	10.5
TRH	11.0	7.1	6.7	8.1
TRW	9.6	8.0	8.2	8.7
CPH	3.0	3.2	3.0	3.0
CPW	2.7	2.2	2.7	2.4
GIR	30.4	21.5	25.8	22.5
P1L	11.3	10.9	10.3	10.8
P1A	11.0	10.9	9.7	10.2
P1B	6.0	6.4	5.2	5.7
P1H	7.5	8.0	8.8	8.1
P1I	6.9	4.8	4.6	5.4
P1P	8.7	7.1	7.0	7.8
P2L	11.3	10.3	11.2	10.8
P2A	5.4	4.8	6.4	6.0
P2B	7.5	7.1	7.3	7.8
P2H	3.0	3.8	3.6	3.0
P2I	4.5	2.9	3.3	3.0
P2P	7.5	6.7	4.9	4.8

Table 1 (cont'd).

Coll. No.	CSIRO H1208-01 Adult female Holotype	CSIRO CA3304 Adult female Paratypes	CSIRO CA4477 Adult male	CSIRO CA4478 Adult male
CLO	–	–	7.3	7.2
CLI	–	–	10.3	10.8
CLB	–	–	1.5	1.5
D1L	8.7	8.7	10.0	9.3
D1A	8.4	8.7	10.0	9.3
D1B	5.7	6.1	7.9	7.2
D1H	4.8	3.8	4.0	4.2
D1I	2.1	2.6	2.7	2.4
D1P	3.9	3.2	2.6	3.3
D2L	8.1	7.7	8.2	8.1
D2A	7.8	7.4	7.9	7.5
D2B	5.7	5.4	5.5	6.0
D2H	3.3	3.5	3.3	3.9
D2I	2.4	2.2	2.4	2.4
D2P	3.3	2.9	2.7	2.7
ANL	12.5	12.5	13.4	13.8
ANA	7.5	7.4	7.0	9.0
ANB	11.0	10.6	11.6	11.1
ANH	3.0	3.5	3.3	3.3
ANI	1.5	1.9	1.8	1.8
ANP	7.2	6.4	7.3	6.6
CDM	25.4	27.6	26.4	27.9
CPV	9.0	8.3	8.2	10.2
CPL+	11.6	15.1	13.4	13.5
CST	3.9	4.2	3.6	4.8
CTR	4.2	4.2	4.0	3.9
CTL	5.4	5.8	5.5	6.0
DAO	6.9	7.1	7.6	7.2
DAI	1.5	1.3	1.8	2.7

Table 2. Vertebral counts, ratios and statistics for *Galeus* specimens examined here. Abbreviations for type specimens: HT – holotype; PT – paratype; SN – syntype.

G. gracilis	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
CSIRO H1208-01 HT	335	36	42	56	78	134	26.8	31.3	41.7	1.2	1.6	141	86
CSIRO CA3304 PT	317	34	41	55	75	130	26.1	31.5	42.3	1.2	1.6	146	133
CSIRO CA4477 PT	329	35	43	–	78	–	–	–	–	1.2	–	133	117
CSIRO CA4478 PT	333	33	41	–	74	–	–	–	–	1.2	–	133	100
range		33	41	55	74	130	26.1	31.3	41.7	1.2	1.6	133	86
		36	43	56	78	134	26.8	31.5	42.3	1.2	1.6	146	133
mean		34.5	41.8	55.5	76.3	132.0	26.5	31.4	42.0	1.2	1.6	138.3	108.9
SD		1.1	0.8	0.5	1.8	2.0	0.4	0.1	0.3	0.0	0.0	5.2	17.8
CV		3.2	2.0	0.9	2.3	1.5	1.3	0.3	0.6	2.4	2.0	3.8	16.4
N		4	4	2	4	2	2	2	2	4	2	4	4

G. arae	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU 66816	289	34	40	59	74	131	25.9	30.5	43.5	1.2	1.7	169	135
SU 66816	272	35	41	57	76	136	25.7	30.1	44.1	1.2	1.7	167	125
ORE 3627	255	36	42	60	78	136	26.4	30.8	42.6	1.2	1.6	162	124
ORE 3627	277	35	41	58	76	136	25.7	30.1	44.1	1.2	1.7	163	130
ORE 3627	270	35	40	60	75	129	27.1	31.0	41.8	1.1	1.5	147	116
ORE 3627	278	36	38	54	74	133	27.0	28.5	44.3	1.1	1.6	141	126
SU 66814	205	35	42	59	77	133	26.3	31.5	42.1	1.2	1.6	164	129
SU 66814	270	35	42	56	77	134	26.1	31.3	42.5	1.2	1.6	153	121
SU 66814	215	34	43	57	77	138	24.6	31.1	44.2	1.3	1.8	170	121
SU 66814	275	35	42	61	77	134	26.1	31.3	42.5	1.2	1.6	156	119
SU 66814	250	36	41	57	77	133	27.0	30.8	42.1	1.1	1.6	140	124
SU 66814	206	35	40	56	75	135	25.9	29.6	44.4	1.1	1.7	164	139
SU 66814	260	35	43	60	78	136	25.7	31.6	42.6	1.2	1.7	147	138
SU 66814	232	35	42	58	77	133	26.3	31.5	42.1	1.2	1.6	146	112
SU 66814	206	35	42	56	77	133	26.3	31.5	42.1	1.2	1.6	167	125
SU 66814	273	36	37	56	73	129	27.9	28.6	43.4	1.0	1.6	139	83
SU 66814	198	35	40	56	75	131	26.3	30.1	43.4	1.1	1.6	160	133
range		34	37	54	73	129	24.6	28.5	41.8	1.0	1.5	139	83
		36	43	61	78	138	27.9	31.6	44.4	1.3	1.8	170	139
mean		35.1	40.9	57.6	76.1	133.6	26.3	30.6	43.1	1.2	1.6	156.0	123.5
SD		0.6	1.6	1.9	1.4	2.4	0.7	0.9	0.9	0.1	0.1	10.4	12.3
CV		1.7	3.9	3.3	1.9	1.8	2.7	3.1	2.1	4.8	4.0	6.7	10.0
N		17	17	17	17	17	17	17	17	17	17	17	17

G. boardmani	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
AMS IA2483 HT	542	37	58	53	95	148	25	39.1	35.8	1.6	1.4	196	121

G. eastmani	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU 35469	342	36	49	65	85	150	24	32.6	43.3	1.4	1.8	140	112
SU 7740 HT	336	33	50	58	83	141	23.4	35.4	41.1	1.5	1.8	159	117

G. melastomus	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU 20604	380	37	46	60	83	143	25.8	32.1	41.9	1.2	1.6	168	119

Table 2 (cont'd).

G. sauteri	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU 21261 ST	370	33	41	54	74	128	25.7	32.0	42.1	1.2	1.6	157	127
SU 21261 ST	362	32	43	53	75	128	25.0	33.5	41.4	1.3	1.7	148	126
SU 21261 ST	369	33	41	51	74	125	26.4	32.8	40.8	1.2	1.5	123	123
SU 21261 ST	366	33	43	49	76	125	26.4	34.4	39.2	1.3	1.5	138	118
CAS 1971-VI:11	382	33	40	49	73	122	27.0	32.7	40.1	1.2	1.5	173	131
CAS 1971-VI:11	383	33	40	50	73	123	26.8	32.5	40.6	1.2	1.5	140	117
CAS 1972-III:14	450	34	39	49	73	122	27.8	31.9	40.1	1.1	1.4	154	123
CAS 34152	303	38	38	56	76	132	28.7	28.7	42.4	1.0	1.5	142	129
CAS 34152	301	32	41	52	73	125	25.6	32.8	41.6	1.3	1.6	144	108
	range	32	38	49	73	122	25.0	28.7	39.2	1.0	1.4	123	108
		38	43	56	76	132	28.7	34.4	41.0	1.3	1.7	173	131
	mean	33.4	40.7	51.4	74.1	125.6	26.6	32.4	41.0	1.2	1.5	146.5	122.4
	SD	1.7	1.6	2.4	1.2	3.1	1.1	1.5	1.0	0.1	0.1	13.1	6.6
	CV	5.1	3.8	4.6	1.6	2.5	4.1	4.5	2.4	7.8	4.9	9.0	5.4
	N	9	9	9	9	9	9	9	9	9	9	9	9

G. schultzi	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
CAS 34852	155	32	41	48	73	121	26.4	33.8	39.6	1.3	1.5	133	120
CAS 34852	143	32	41	51	73	124	25.8	33.0	41.1	1.3	1.6	157	100
CAS 33843	177	33	44	53	77	130	25.3	33.8	40.7	1.3	1.6	167	136
CAS 34556	165	33	47	48	80	128	25.7	36.7	37.5	1.4	1.5	175	127
CAS 34556	182	35	44	57	79	136	25.7	32.3	41.9	1.3	1.6	142	131
	range	32	41	48	73	121	25.3	32.3	37.5	1.3	1.5	133	100
		35	47	57	80	136	26.4	36.7	40.2	1.4	1.6	175	136
	mean	33.0	43.4	51.4	76.4	127.8	25.8	34.0	40.2	1.3	1.6	154.8	122.9
	SD	1.1	2.2	3.4	2.9	5.2	0.3	1.5	1.5	0.1	0.1	15.4	12.6
	CV	3.3	5.2	6.6	3.8	4.0	1.3	4.4	3.8	4.5	4.3	10.0	10.3
	N	5	5	5	5	5	5	5	5	5	5	5	5

Hemitriakis falcata n.sp. and *H. abdita* n.sp., Two New Houndsharks (Carcharhiniformes: Triakidae) from Australia

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ABSTRACT. Two new species of the genus *Hemitriakis* Herre, 1923 (Carcharhiniformes: Triakidae) are described from tropical Australia. *Hemitriakis falcata* is described from ten specimens from the outer continental shelf of Western Australia at depths of 146 to 197 m. *Hemitriakis abdita* is described from five specimens from the Coral Sea Plateau off north-eastern Queensland at 225 to 401 m. *Hemitriakis falcata* and *H. abdita* are separable from their two named congeners *H. leucoperiptera*, from the Philippine Islands, and *H. japanica*, from Japan, Taiwan, China and Korea, by a combination of vertebral counts, first dorsal position, fin and eye shape, and juvenile colouration. *Hemitriakis falcata* additionally differs from *H. japanica* in chondrocranial morphology. *Hemitriakis falcata* and *H. abdita* are sibling species separated by wide, non-overlapping differences in vertebral counts as well as by slight differences in morphometrics, tooth counts, colouration, and cranial morphology. These species represent the first record of *Hemitriakis* from Australia. A nominal record of *H. japanica* from Ambon is uncertain while another record of *H. japanica* from New Caledonia may be based on *H. abdita*. A key to species of *Hemitriakis* is presented.

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Recent trawl collections on the outer continental shelves and upper slopes of Australia have yielded numerous sharks and other chondrichthians (Gloerfelt-Tarp & Kailola, 1984; Davis & Ward, 1984; Sainsbury *et al.*, 1985; Gorman & Graham, 1985; Williams, 1987). Included in this material are specimens of houndsharks (Carcharhiniformes: Triakidae) that represent the first Australian records of the genus *Hemitriakis* Herre, 1923 as defined by Compagno (1970).

Compagno (1984) noted an undescribed species of *Hemitriakis* from Western Australia while Compagno (1988) cited two specimens of this species (WAM P26271-001 and WAM P26724-007) and deferred their description to the present paper. While preparing the description of this species we discovered that additional specimens of *Hemitriakis* deposited in the CSIRO

collections fell into two non-overlapping groups on vertebral counts, with an average difference of 27 centra in total counts between the groups. The higher vertebral count group is represented by five specimens from the upper slope on the Coral Sea Plateau off north-eastern Queensland while the lower count group includes eight specimens from Western Australia along with the material cited by Compagno (1988). As the two groups included individuals of both sexes that are very similar in morphology and are clearly separable from the western North Pacific *H. japanica* (Müller & Henle, 1839) and *H. leucoperiptera* Herre, 1923, they are regarded as a pair of undescribed sibling species.

Terminology and Abbreviations

The terminology for external structures, chondrocrania, vertebrae and dentition follows Compagno (1970, 1988). The abbreviations for tooth row groups include: AL – anterolaterals; AP – anteroposteriors; M – medials; P – posteriors. For tooth counts (Table 3 [Appendix]), the abbreviations include: TT – total number of tooth rows in both jaws; UT – number of upper tooth rows; LT – number of lower tooth rows. For vertebrae, the abbreviations include: MP – monospondylous precaudal centra; DP – diplospondylous precaudal central; DC – diplospondylous caudal centra; TC – total vertebral counts (MP + DP + DC counts). An additional abbreviation is: PC – precaudal (MP + DP) vertebral counts.

The abbreviations and methods of measuring follow the FAO system of Compagno (1984), except that the measurement MOL (mouth length) was incorrectly shown in the diagram (Compagno, 1984: 12) as extending from the lower symphysis to the mouth corners; it should be from the *upper* symphysis to the mouth corners. Also, TL is used for total length and PCL for precaudal length (following general usage in ichthyology) instead of TOT and PRC. The abbreviations for measurements in this account include: TL (TOT) – total length; PCL (PRC) – precaudal length; PRN – prenarial length; POR – preoral length; POB – preorbital length; PSP – prespiracle length; PGI – pregill (prebranchial) length; HDL – head length; PP1 – prepectoral length; PP2 – prepelvic length; SVL – snout-vent length; PAL – preanal length; PD1 – pre-first dorsal length; PD2 – pre-second dorsal length; IDS – interdorsal space; DCS – dorso-caudal space; PPS – pectoral-pelvic space; PAS – preanal space; ACS – anal-caudal space; EYL – eye length; EYH – eye height; INO – interorbital width; NOW – nostril width; INW – internarial width; ANF – anterior nasal flap length; SPL – spiracle length; ESL – eye-spiracle length; MOL – mouth length; MOW – mouth width; ULA – upper labial furrow length; LLA – lower labial furrow length; GS1 – first gill opening height; GS2 – second gill opening height; GS3 – third gill opening height; GS4 – fourth gill opening height; GS5 – fifth gill opening height; HDH – head height; HDW – head width; TRH – trunk height; TRW – trunk width; CPH – caudal peduncle height; CPW – caudal peduncle width; GIR – girth; P1L – pectoral length; P1A – pectoral anterior margin; P1B – pectoral base; P1H – pectoral height; P1I – pectoral inner margin; P1P – pectoral posterior margin; P2L – pelvic length; P2A – pelvic anterior margin; P2B – pelvic base; P2H – pelvic height; P2I – pelvic inner margin; P2P – pelvic posterior margin; CLO – clasper outer length; CLI – clasper inner length; CLB – clasper base width; D1L – first dorsal length; D1A – first dorsal anterior margin; D1B – first dorsal base; D1H – first dorsal height; D1I – first dorsal inner margin; D1P – first dorsal posterior margin; D2L – second dorsal length; D2A – second dorsal anterior margin; D2B – second dorsal base; D2H – second dorsal height; D2I – second dorsal inner margin; D2P – second dorsal posterior margin; ANL – anal length; ANA – anal anterior margin; ANB – anal base; ANH – anal height; ANI – anal inner margin; ANP – anal posterior margin; CDM – dorsal caudal margin; CPV – preventral caudal margin; CPL – lower postventral caudal margin; CPU – upper postventral caudal margin; CST – subterminal caudal margin; CTR – terminal caudal margin; CTL – terminal caudal lobe; DPI – first dorsal midbase-pectoral insertion; DPO – first dorsal midbase-pelvic origin; PDI – pelvic midbase-first dorsal insertion; PDO – pelvic midbase-first dorsal origin; DAO – second dorsal-anal origin; DAI – second dorsal-anal insertion; FOR – fork length (snout tip to caudal fork).

NBL is the abbreviation for nasobasal length, the distance from the base of the medial rostral cartilage to the occipital centrum of the chondrocranium. WT is the abbreviation for weight in g. Abbreviations for sex and maturity are after Compagno (1988) and include: SEX/M – sex and maturity stages: F – female; M – male; 1 – fetus; 2 – immature; 3 – adolescent; 4 – adult. Abbreviations for statistics include: CV – coefficient of variation; N – number of specimens; SD – standard deviation; SE – standard error.

Abbreviations and prefixes for field, accession, and catalog numbers follow Leviton *et al.* (1986) and Compagno (1988) in part: CAS – CAS-Acc., California Academy of Sciences, San Francisco; CSIRO CA and H – CSIRO Marine Laboratories, Hobart, Tasmania; LACM-F – Los Angeles County Museum of Natural History, uncatalogued Applegate specimens; LJVC – L.J.V. Compagno collection; SO – CSIRO RV *Soela* station number; SU – Stanford University fish collection, now housed at CAS; UMMZ – University of Michigan Museum of Zoology, Ann Arbor; USNM – United States National Museum of Natural History, Washington, D.C.; WAM – Western Australian Museum, Perth.

All tables are listed in the Appendix.

Triakidae Gray, 1851

Comments. For definitions of this family see Compagno (1973a, 1973b, 1979, 1984, 1988).

Hemitriakis Herre, 1923

Hemitriakis Herre, 1923: 70. Type species *Hemitriakis leucoperiptera* Herre, 1923, by original designation.

Comments. For detailed definitions and discussions of the scope of this genus see Compagno (1970, 1979, 1984, 1988). *Hemitriakis* was proposed by Herre (1923) as a monotypic genus for *H. leucoperiptera* Herre, 1923, from the Philippine Islands. *Hemitriakis leucoperiptera* was included in *Triakis* Müller & Henle, 1838 by Fowler (1941), Bigelow & Schroeder (1948), Garrick (1954), Kato (1968), Springer (1968), and Pinchuk (1972), but was revived by Compagno (1970) for Herre's species and *Galeus japanicus* Müller & Henle, 1839. *Hemitriakis japanica*, from off China, Korea, Taiwan and Japan, had been placed in the genus *Galeorhinus* or its synonyms by previous writers. The genus *Hemitriakis* was recognised by Compagno (1973a, 1973b, 1979, 1984, 1988), Steuben & Krefft (1978, 1989), Cadenat & Blache (1981), and Masuda *et al.* (1984).

There is probably a second species of *Hemitriakis* in Philippine waters, differing from *H. leucoperiptera* in colouration and fin proportions (Compagno, 1970, 1979, 1988: fig.17.11C) and also vertebral counts (see discussion below). The smaller paratypes of *Hemitriakis falcata* n.sp. and *H. abdita* n.sp. have a similar spotted colour pattern to this species (Fig.2), except that their dark spots and saddles lack light centres.

Fowler (1941) cited a record of *Hemitriakis japanica* from Ambon, while Fourmanoir & Rancurel (1972) reported *H. japanica* from New Caledonia. We have not been able to verify the Ambon record, but a large New Caledonian *Hemitriakis* was deposited by P. Fourmanoir in the Museum National d'Histoire Naturelle, Paris, as *Galeorhinus japanicus*. We have examined photographs, measurements and radiographs of this specimen that were prepared for us through the kind agency of Drs B. Seret and M.-L. Bauchot. This specimen has a much higher vertebral count than all other *Hemitriakis* except *H. abdita* and may represent another undescribed species of *Hemitriakis* (see discussion below) or possibly may be an adult of *H. abdita*.

Comparative Material

Hemitraikis japanica. JAPAN: LACM F-420, 350 mm immature male; LACM F-421, 582 mm immature female; SU 12677, 682 mm immature female, Nagasaki; UMMZ 179060, 650 mm immature male, Auraji (Osaki Market, Osaki); UMMZ 179061, 560 mm immature female, Ainoshima (Fukuoka Market, Fukuoka); UMMZ 179062, 505 mm immature male, Ezumi (Ezumi Market); LJVC-0419, 898 mm adult male; LJVC-0420, 886 mm adult male; LJVC-0421, 833 mm adolescent male (heads only); East China Sea. TAIWAN: USNM 191193, 685 mm eviscerated female, 651 mm immature male, 675 mm adult male, Taipei-hsien; CAS Acc. 1971-VII: 16, 235 mm immature female, Taiwan Straits, about 26°N 121°E; CAS Acc. 1971-VII: 22, 220 mm immature female, Taiwan Straits, 27.5°N 121°E; CAS 28576, 2 immature males, 252-307 mm, 353 mm immature female, Taiwan Straits.

Hemitriakis leucoperiptera. SU 27118, 169 mm male and 170 mm female fetuses, Dumaguete, Negros Island, Philippine Islands.

Hemitriakis sp. SU 40097, 171 mm male fetus and 3 female fetuses, 161-180 mm, Dumaguete, Negros Island, Philippine Islands.

Hemitriakis sp. near *abdita*. MNHN 1986-720, 860 mm adult male, New Caledonia.

Key to the Species of *Hemitriakis*

1. Eyes relatively low and slitlike. First dorsal origin over or behind pectoral free rear tips. Fins not strongly falcate in adults ..... *Hemitriakis japanica* (Müller & Henle, 1839)

—— Eyes relatively high and horizontally oval. First dorsal origin anterior to pectoral free rear tips. Fins strongly falcate in adults 2

2. Total vertebral counts 133-146, MP counts 34-35. Young without dark bars and spots on precaudal fins and body ..... *Hemitriakis leucoperiptera* Herre, 1923

—— Total vertebral counts 158-193, MP counts 37-53. Young with prominent dark bars and spots on precaudal fins and body 3

3. No dusky bar on the ventral surface of the snout. Total vertebral counts 158-165, MP counts 37-41, DP counts 55-60 ..... *Hemitriakis falcata* n.sp.

—— A dusky bar on the ventral surface of the snout. Total vertebral counts 186-193, MP counts 48-53, DP counts 77-78 ..... *Hemitriakis abdita* n.sp.

Hemitriakis falcata n.sp.

Sicklefin houndshark

Figs 1-5, 6A,C,E

Type material. HOLOTYPE, WAM P26271-001 (Fig.1), 770 mm adult male, RV *Courageous* stn CR-78-755, 29 June, 1978, bottom trawl, 16°54'S 120°50'E, Western Australia, outer continental shelf at 150 m depth.

PARATYPES, WAM P26274-007 (Fig.2), 258 mm immature female, RV *Courageous* 30 May 1978, 18°11'S 118°57'E, 215 km north to north-north-east off Port Hedland, WA, 160 m depth, bottom trawl; CSIRO H1094-01, SO7/87/133, 380 mm immature male, 13 Oct. 1987, 18°58'S 117°34'E, 146 m, silt bottom; CSIRO CA4056, SO1/83/23, 251 mm immature male, 25 Jan. 1983, 19°09'S 116°59'E, 180 m, silt bottom; CSIRO H1036-26, SO7/87/129, 773 mm adult male, 12 Oct. 1987, 19°06'S 117°08'E, 181 m, silt bottom, North West Shelf, WA; CSIRO H1035-17, SO6/86/84, 724 mm adult male, 24 Oct. 1986, 19°09'S 116°53'E, 197 m, shelly sand bottom, North West Shelf, WA (head and claspers dissected); CSIRO H977-01, SO6/86/109, 744 mm adult male, 28 Oct. 1986, 19°34'S 115°52'E, 147 m; CSIRO H1035-16, SO6/86/84, 740 mm adult male, 24 Oct. 1986, 19°09'S 116°53'E, 197 m, shelly sand bottom, North West Shelf, WA; CSIRO H1036-27, SO7/87/129, 760 mm adult male, 12 Oct. 1987, 19°06'S 117°08'E, 181 m, silt bottom, North West Shelf, WA; CSIRO H1035-18, SO6/86/84, 695 mm adult male, 24 Oct. 1986, 19°09'S 116°53'E, 197 m, shelly sand bottom, North West Shelf, WA.

Diagnosis. *Hemitriakis* with eyes horizontally oval. Tooth rows 55-66 in both jaws. Dorsal, pectoral and anal fins strongly falcate in adults. First dorsal-fin origin anterior of free rear tips of pectoral fin, over pectoral-fin insertions. Total vertebral counts 158-165, precaudal counts 101-109, monospondylous precaudal counts 37-41. Newborn young and subadults below 500 mm with bold to faint colour pattern of saddles and large spots on body and fins; spots with solid centers. Males fully mature at 695-773 mm TL.

Etymology. From Latin *falcata*, sickle-shaped, in reference to the highly curved fins of adults.

Description. Proportional dimensions as percentage of total length (see terminology) for type series, listed in Table 1.

Head short, length 0.8-1.1 in pectoral-pelvic space; fairly narrow, flattened, and roughly trapezodial in cross-section at eyes. Outline of head in lateral view slightly

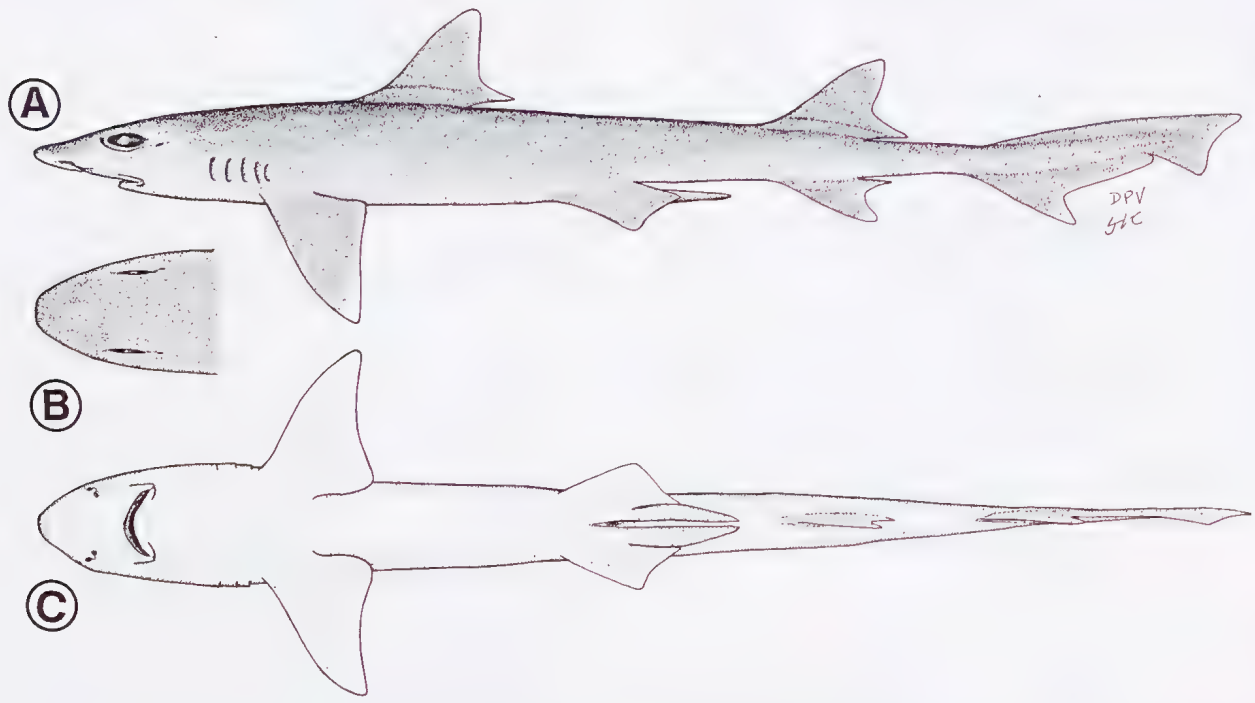

Fig.1. *Hemitriakis falcata* n.sp., holotype, WAM P26271-001, 770 mm adult male; A, lateral and C, ventral views; B, dorsal view of head. Illustration by D.P. Voorfelt and L.J.V. Compagno.

convex or nearly straight dorsally, slightly convex ventrally along lower jaws and nearly flat beneath gills; in dorsoventral view head anteriorly parabolic and posteriorly tapering along branchial region. Preoral snout long, 1.1-1.3 in mouth width. Snout tip narrowly rounded in dorsoventral view, with shallow indentations anterior to nostrils; snout bluntly pointed in lateral view, convex above and below.

External eye opening with prominent posterior notch but no anterior one; eyes large and elongate-oval in shape, eye length 4.1-6.5 in head length, eye length 1.9-3.0 times eye height. Eyes dorsolateral on head, with lower edges well medial to horizontal head rim in dorsal view, subocular ridges prominent. Nictitating lower eyelids external in young and adults, with deep but entirely scaled subocular pouches and secondary lower eyelids.

Spiracles small, length 4.6-11.5 in eye length, spiracles 0.1-0.3 eye lengths behind and below posterior eye notch. First four gill openings about equally high or first slightly lower than others; fifth shorter than third, height of fifth 0.6-0.8 of third; third 7.2-11.8 in head and 0.4-0.8 of eye length. All gill openings slightly concave, gill filaments not visible from outside. Upper ends of gill openings slightly below lower edges of eyes. Gill-raker papillae absent from gill arches.

Nostrils with large oval incurrent apertures lacking posterolateral keels, rounded anterior nasal flaps with round or bluntly pointed tips, prominent mesonarial flaps, small oval excurrent apertures, and small posterior nasal flaps. Nostrils well in front of mouth, 2.0–3.3 times farther from snout tip than from eyes. Nostril width 2.0-3.0 in internarial space, 1.8-3.0 in eye length, 0.8-1.7 in third gill opening height.

Mouth broadly arched, moderately large, short, mouth width about 0.7 of head width at mouth corners, 2.7-3.5 in head length; mouth length 2.2-2.7 in mouth width. Tongue large, flat and broadly rounded, filling floor of mouth. Maxillary valve narrow, width slightly more than five in eye diameter; valve covered with small papillae. No buccal papillae on floor of mouth and palate behind maxillary valve, this smooth and covered with buccopharyngeal denticles. Labial furrows long, upper 1.3-2.0 times lower furrows, anterior ends of uppers under first third of eye length and reaching virtually to symphysis of upper jaw. Labial cartilages large.

Teeth relatively few, in 29-35/26-33 rows (see Table 3 for detailed counts and statistics). Teeth not arranged in diagonal files, no toothless spaces at symphysis. Teeth weakly differentiated in upper and lower jaws and along jaws, with well-defined medials and weakly differentiated anterolaterals and posteriors. Tooth formulae (count ranges combined for both sides of jaw) are:

$$\frac{\text{M3-5 AL8-14 P1-5}}{\text{M3-5 AL5-10 P3-9}} \quad \text{or} \quad \frac{\text{M3-5 AP12-15}}{\text{M3-5 AP11-14}}$$

Upper anterolateral teeth higher-crowned than lowers (Fig.3), both with well-developed distal cusplets and oblique cusps, cusps somewhat higher and more erect on upper teeth than lowers; small juveniles have anterolateral teeth with blade only and no cusplets, but later juveniles, subadults and adults acquire 1-3 cusplets on successive generations of teeth (compare Fig.3B,C,E with G,H). Medial teeth smaller than anterolaterals, with more erect cusps, higher crowns, and both mesial and distal cusplets (Fig.3A). Anterolaterals gradually become lower crowned and lower-cusped along the dental band, grade into keel-like posterior teeth which are very low-crowned, lack cusps,

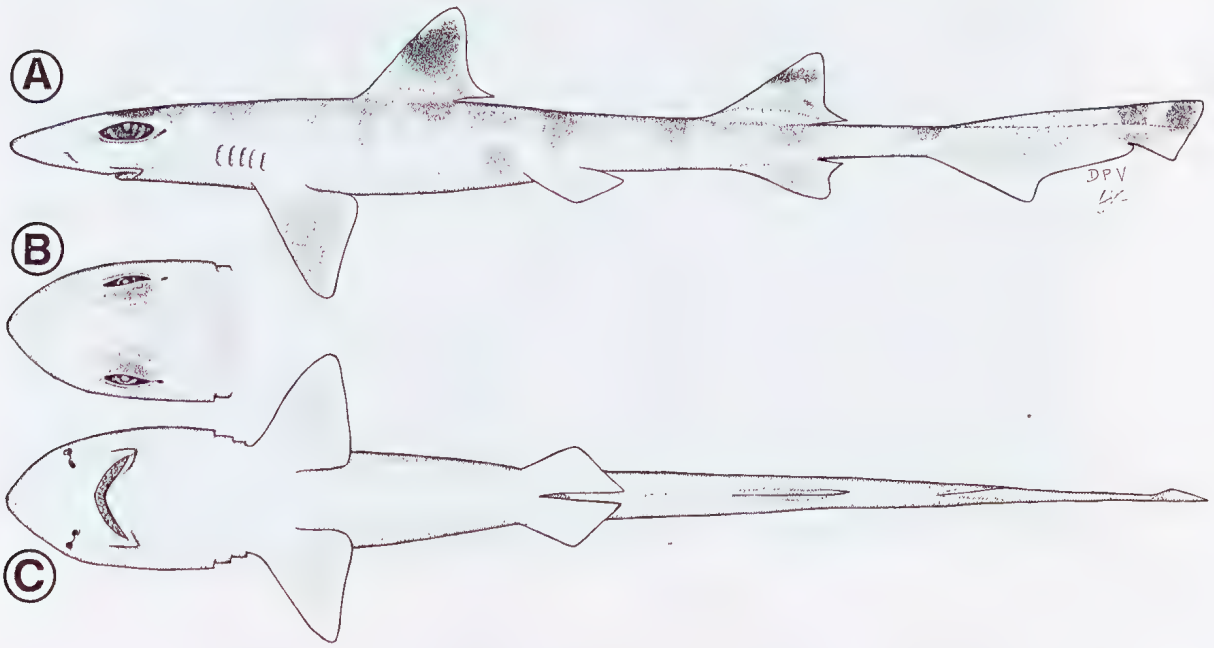

Fig.2. *Hemitriakis falcata* n.sp., paratype, WAM P26274-007, 258 mm immature female, A, lateral and C, ventral views; B, dorsal view of head. Illustration by D.P. Voorfelt and L.J.V. Compagno.

have a broad convex edge (Fig.3D). All teeth have broad basal ledges, strong basal grooves, large mesial and distal root lobes separated by broad transverse grooves and prominent centrolingual foramen on linguobasal attachment surface of roots, medial teeth with lateral foramina. Transverse ridges obsolete on teeth of specimens examined, perhaps represented by irregular notching on basal ledge. Tooth histological type orthodont as observed with transmitted light through teeth in water, with a definite pulp cavity, crown formed of orthodentine and enameloid, osteodentine confined to roots.

Body elongate, slender, trunk vertically oval to circular in section at first dorsal-fin base, length of trunk from fifth gill openings to vent 1.0-1.5 times head length. A low interdorsal ridge on midline of back between dorsal fins, and a low postdorsal ridge, but without predorsal ridges; lateral ridges absent from body. Caudal peduncle slender, cylindrical-tapering and without lateral keels, caudal peduncle height at upper caudal-fin origin 0.9-1.5 of width there, 4.2-5.0 in dorsal-caudal space. Precaudal pits absent.

Lateral trunk denticles with elongated, teardrop-shaped crowns about 1.5 times as long as wide in adults (Fig.4A) but up to twice as long as wide in young (Fig.4B). Interspaces between ridges, including that between medial ridges, covered with reticulated depressions which are better developed in young than adults. Crown with a single medial ridge along the entire crown length in the smallest denticles of newborn young, but larger denticles in young and all denticles in larger juveniles and in adults have prominent paired longitudinal ridges that diverge and then converge posteriorly to end at the medial cusps. Medial cusps relatively long and strong, a third to half length of crown but relatively longer in young than adults. Pair of strong lateral ridges on crown, terminating in strong but short lateral cusps. Denticle crowns closely imbricated in adults and larger juveniles

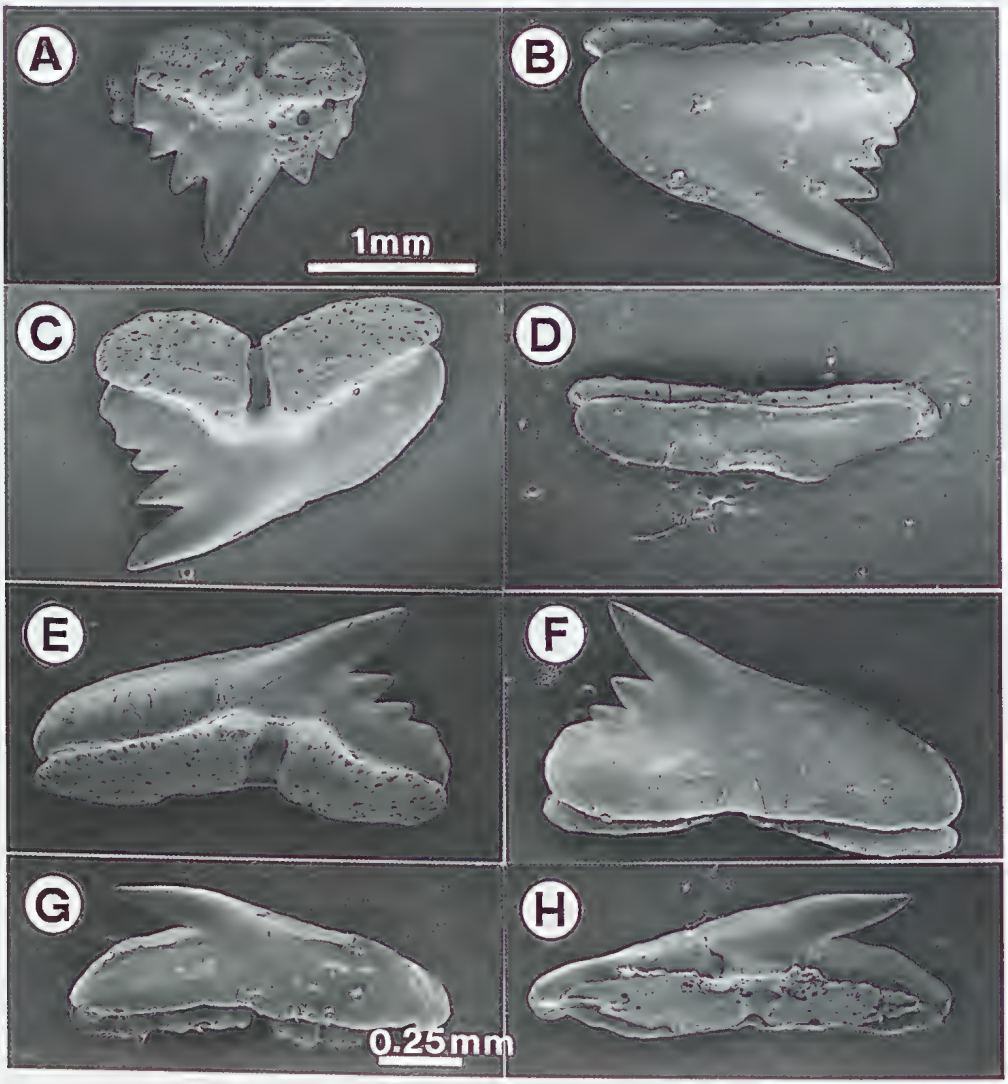

Fig.3. *Hemitriakis falcata*, scanning electron micrographs of representative teeth. A-F, CSIRO H1035-17, 724 mm adult male. A, upper medial tooth, lingual view; B, first upper anterolateral tooth, labial view; C, 2nd upper anterolateral tooth, lingual view; D, 2nd upper posterior tooth, labial view; E, second lower anterolateral tooth, lingual view; F, third lower anterolateral tooth, labial view. G-H, CA4056, 251 mm immature male, lower anterolateral teeth from near symphysis. G, labial view; H, lingual view. A-F, scale bar = 1 mm; G-H, scale bar = 0.25 mm. Photos by A.J. Rees.

but wide spaced in smallest young.

Pectoral fins narrow and semifalcate, with broadly convex anterior margins, bluntly to acutely pointed apices, nearly straight (young) to broadly concave (adults) posterior margins, broadly rounded free rear tips, convex inner margins, narrow bases. Pectoral-fin anterior margin 1.2-1.6 times pectoral-fin length. Pectoral fins subequal in area to first dorsal fin. Origins of pectoral fins under fourth gill openings. Apex of pectoral fin posterior to its free rear tip when fin is elevated and adpressed to body.

Pectoral fin skeleton with radials extending about 0.6 of pectoral anterior margin length into fin. Radials mostly divided into 3 segments except for bisegmental propterygial radial and last 2 metapterygial radials. Longest distal radial segment 1.3 times length of its proximal segment. Distal pectoral-fin radials with parallel edges and truncated tips, not pointed and tapering. No fusion of proximal radial segments. Pectoral-fin skeleton tribasal, propterygium with a single radial, mesopterygium with 3 radials, metapterygium with 10 radials on basal segment and 4 on metapterygial axis; total radial count 18 in one adult counted. Propterygium short, narrow and slightly elongated in the axis of its radial. Mesopterygium short, subquadrate, and slightly expanded distally in the axes of its radials. Metapterygial basal segment triangular, elongated diagonal to the axes of its radials; metapterygial axis short, trisegmental, and with length about two-thirds of metapterygial basal segment.

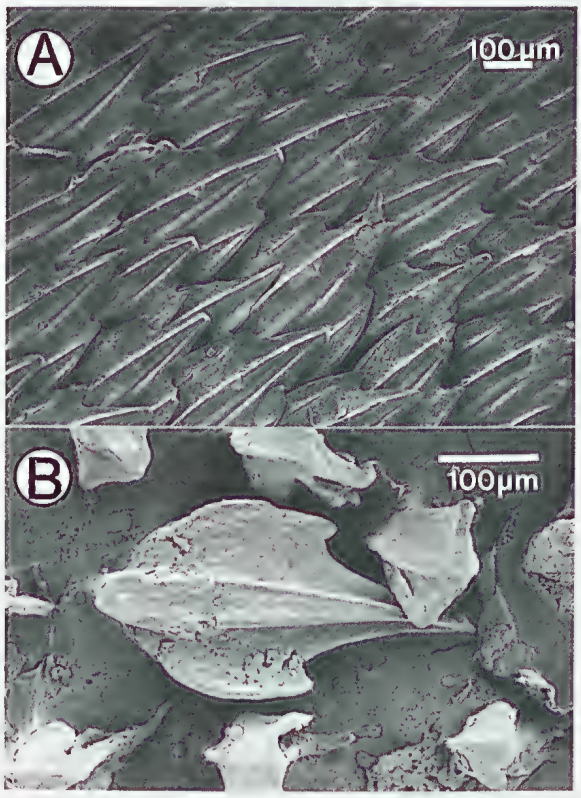

Fig.4. *Hemitriakis falcata*, scanning electron micrographs of lateral trunk denticles. A, denticles in three-quarters anteriolateral view from CSIRO H977-01, 744 mm adult male; B, crown of denticle from CA4056, 251 mm immature male, surrounded by broken pedicels. Photos by A.J. Rees.

Pelvic fins broadly triangular and weakly falcate in adults but not falcate in young; pelvic-fin anterior margins 0.4-0.6 of pectoral-fin anterior margins; area subequal to anal-fin area. Pelvic-fin anterior margins slightly convex, apices bluntly pointed (adults) or narrowly rounded (young), posterior margin straight (young) or broadly concave (adults), free rear tips pointed, inner margins straight.

Claspers relatively long and basally stout, convex and strongly tapering on lateral edge, with a convex, blunt-tipped clasper glans (Fig.5A). Claspers extending well behind pelvic-fin free rear tips, by distance about 1.3 times pelvic-fin inner margin, but falling in front of anal-fin origin by about length of anal-fin base. Most of clasper except dorsal surface of glans covered with small clasper denticles with blunt, rounded crowns and no cusps. Exorhipidion, envelope and pseudopera absent, clasper groove open. Rhipidion present, very large, extending over most of length of clasper glans, formed as a flat, convex-edged blade with posterior end far behind cover rhipidion. Cover rhipidion very low, hardly differentiated from medial edge of clasper groove, extending from apopyle to apex of rhipidion. Pseudosiphon very short, slitlike, extending opposite the posteriormost third of the cover rhipidion. Clasper siphons very long and narrow, extending anteriorly along the entire abdomen and terminating about opposite the last third of the pectoral-fin bases; width of siphons at pelvic-fin origins about two-thirds of distance from midline of body to pelvic-fin origin.

Clasper skeleton simple (Fig.5B-D). Axial cartilage or appendix-stem connected proximally by a single very short basal segment (B1) and a moderately long, posteriorly tapering, wedge-shaped dorsal beta cartilage (ß) to pelvic basipterygium. Clasper shaft, formed from axial cartilage and tightly rolled dorsal and ventral marginal cartilages, is slender, tapers and then expands slightly posteriorly in an elongated hourglass-shape. Clasper glans skeleton comprises a large, narrow, subrectangular, slightly curved, blunt-tipped dorsal terminal and a more proximally expanded, blade shaped ventral terminal, articulating with and separated along their proximomesial nine-tenths to the tapering, fairly narrow, cylindrical-flattened end-style (terminal extension of axial cartilage); very short free posterior ends of terminal cartilages separated by a narrow gap and are nearly straight. Accessory dorsal marginal cartilage (RD2) a long, elongate-oval, proximodistally tapering cartilage that supports the weak cover rhipidion. Accessory dorsal terminal cartilage (TD2) a large, elongated, bladelike, distally tapering cartilage that extends along proximal two-thirds of clasper glans from dorsal marginal to midlength on ventral terminal, supports the rhipidion. No ventral covering piece, unlike some other triakids, nor accessory ventral terminal cartilages. Very long, narrow, broad-tipped, bladelike accessory terminal cartilage (T3) present, extends from hypopyle just anterior to RD2 end to midlength of TD2 and just posterior to RV-TV junction.

First dorsal fin high, apically narrow and falcate, with basally concave and distally convex anterior margin, narrowly rounded apex, broadly concave posterior margin, acutely pointed free rear tip, and nearly straight inner margin. First dorsal-fin origin slightly anterior to free rear tips of pectoral fins, midpoint of base varies from 1.1 times closer to pelvic-fin origins than pectoral-fin insertions to 1.8 times closer to pectoral-fin insertions than pelvic-fin origins. First dorsal-fin insertion and free rear tip well anterior to pelvic-fin origins. Posterior margin slanting ventrally (young) or anteroventrally (adults) from apex, then abruptly posteriorly towards free rear tip, insertion slightly anterior (adults) to posterior (young) to level of dorsal apex. First dorsal-fin base 2.2-2.8 in interdorsal space, 2.0-2.4 in dorsal caudal-fin margin; first dorsal-fin height 1.1-1.6 in first dorsal-fin base; first dorsal-fin inner margin 1.5-2.1 in first dorsal-fin height, 2.1-2.6 in first dorsal-fin base.

Second dorsal fin high, apically narrow and falcate, nearly as large as first dorsal fin, second dorsal-fin height 0.7-1.0 in first dorsal-fin height, second dorsal-fin base 0.8-1.0 of first dorsal-fin base. Second dorsal fin with basally concave and apically convex anterior margin, narrowly rounded apex, deeply concave posterior margin, acutely pointed free rear tip, and straight or slightly concave inner margin. Second dorsal-fin origin separated from pelvic-fin insertions by a space about 1.8-2.6 times pelvic-fin base; free rear tip extending slightly behind anal-fin free rear tip but far in front of upper caudal-fin origin. Posterior margin extending ventrally (young) or anteroventrally (adults) from apex, then abruptly posteroventrally towards free rear tip, insertion slightly anterior (adults) to about opposite (young) to dorsal apex. Second dorsal-fin base 1.1-1.3 in dorsocaudal space, second dorsal-fin height 1.3-1.8 in second dorsal-fin base, second dorsal-fin inner margin 1.6-2.0 in second dorsal-fin height and 2.2-3.0 in second dorsal-fin base.

Anal fin low, apically narrow, semifalcate, much smaller than second dorsal fin, anal-fin height 0.5-0.6 in second dorsal-fin height, anal-fin base 0.7-1.0 in second dorsal-fin base. Anterior margin concave basally and distally convex, apex bluntly rounded (young) to sharply pointed (adults), posterior margin deeply concave (young) to broadly notched (adults), free rear tip acutely pointed, inner margin nearly straight. Anal-fin base with short preanal ridges less than one-third of rest of

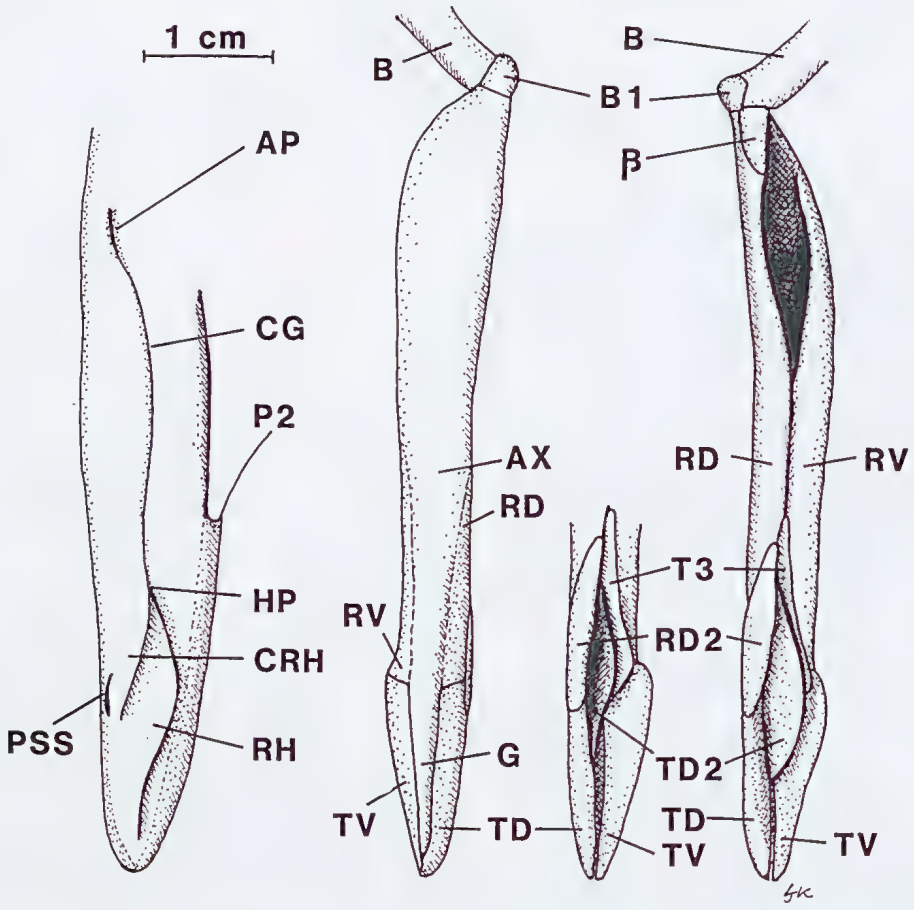

Fig.5. *Hemitriakis falcata*, morphology of right clasper, CSIRO H1035-17, 724 mm adult male. A, dorsal view of entire clasper. B-D, clasper skeleton. B, ventral view; C, dorsal view of entire clasper skeleton, terminal elements not dilated; D, clasper glans with elements spread. Abbreviations: AP – apopyle; AX – axial cartilage; ß – beta cartilage; B – basipterygium; B1 – intermediate segment; CG – clasper groove; CRH – cover rhipidion; G – end-style; HP – hypopyle; P2 – pelvic fin; PSS – pseudosiphon; RD – dorsal marginal cartilage; RD2 – accessory dorsal marginal cartilage; RH – rhipidion; RV – ventral marginal cartilage; T3 – accessory terminal cartilage; TD – dorsal terminal cartilage; TD2 – dorsal terminal 2 cartilage; TV – ventral terminal cartilage. Illustration by L.J.V. Compagno.

base, anal-fin origin slightly behind second dorsal-fin origin by 0.1-0.3 of second dorsal-fin base, anal-fin insertion slightly behind, approximately below, or slightly in front of second dorsal-fin insertion. Anal-fin free rear tip well in front of lower caudal-fin origin. Anal-fin posterior margin slanting dorsally (young) or anterodorsally (adults) from apex, then abruptly posterodorsally towards free rear tip, anal-fin insertion in front of apex. Anal-fin base 1.0-1.9 in anal-caudal space, anal-fin height 1.7-2.6 in anal-fin base, anal-fin inner margin 1.0-1.6 in anal-fin height and 2.1-3.2 in anal-fin base.

Caudal fin narrow-lobed and asymmetrical, with short terminal lobe and prominent ventral lobe at all stages, bluntly angular in young but strongly falcate in adults. Caudal fin short, dorsal caudal-fin margin 3.6-3.9 in precaudal length. Preventral caudal-fin margin 1.9-2.4 and terminal lobe length 2.6-3.1 in dorsal caudal-fin

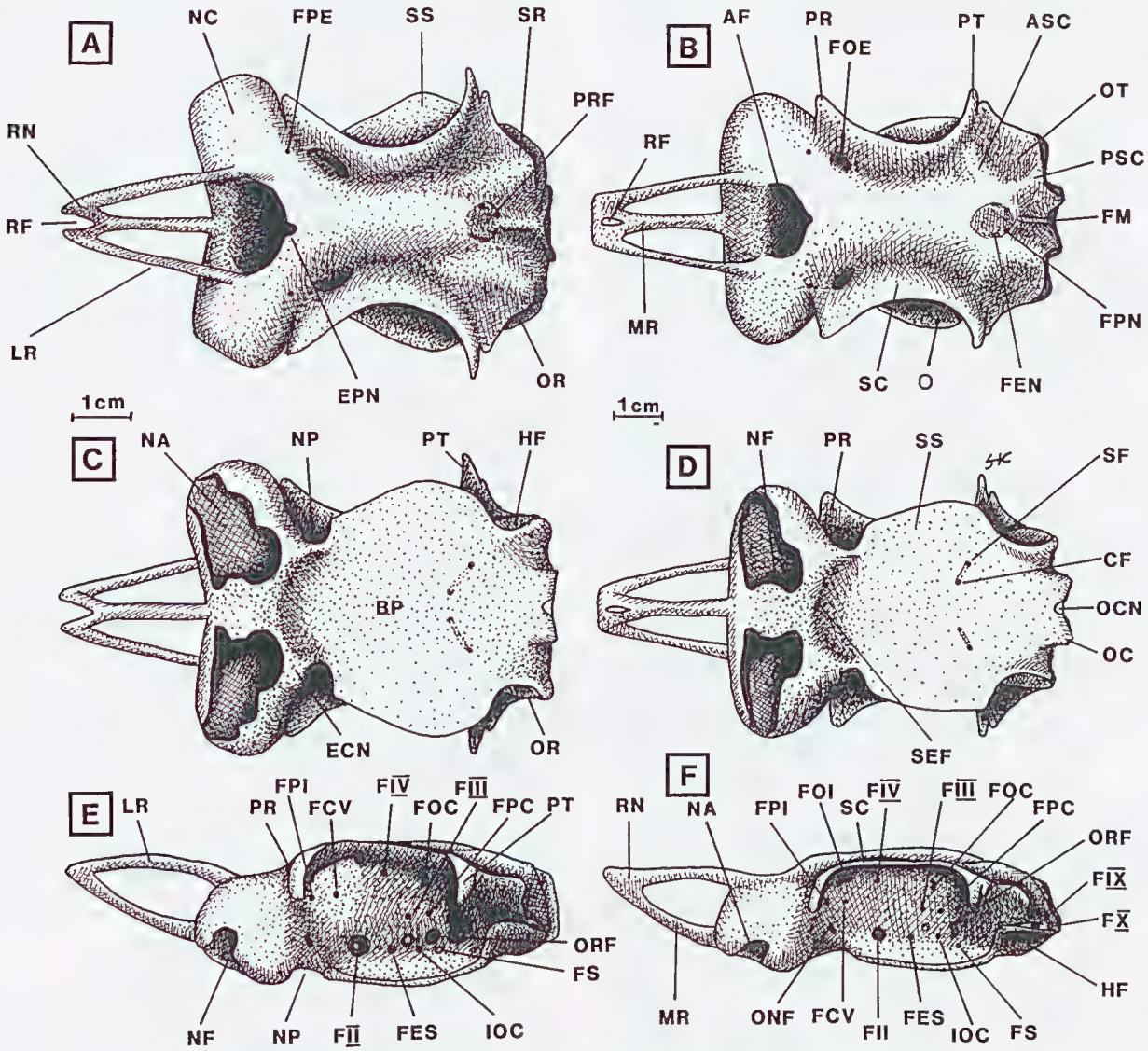

Fig.6. *Hemitriakis* spp., chondrocrania. A,C,E – *H. falcata*, CSIRO H1035-17, 724 mm adult male, cranium. A, dorsal view; C, ventral view; E, lateral view. B,D,F – *H. japanica*, LJVC-0420, 886 mm adult male, cranium. B, dorsal view; D, ventral view; F, lateral view. Abbreviations: AF – anterior fontanelle; ASC – anterior semicircular canal; BP – basal plate; CF – internal carotid foramen; ECN – ectethmoid condyle; EPN – epiphysial notch; FCV – foramen for anterior cerebral vein; FEN – endolymphatic foramen; FES – foramen for efferent spiracular artery; FM – foramen magnum; FOC – foramen for superficial opthalmic nerve; FPC, FPE and FPI – cranial, external and orbital foramina of deep ophthalmic nerve; FPN – perilymphatic foramen; FII – optic nerve foramen; FIII – oculomotor nerve foramen; FIV – trochlear nerve foramen; FIX – glossopharyngeal nerve foramen; FX – vagus nerve foramen; HF – hyomandibular facet; IOC – interorbital canal; LR – lateral rostral cartilage; MR – medial rostral cartilage; NA – nasal aperture; NF – nasal fontanelle; NC – nasal capsule; NP – orbital notch; O – orbit; OC – occipital condyle; OCN – occipital centrum; ONF – orbitonasal foramen; OR – opisthotic ridge; ORF – orbital fissure; OT – otic capsule; PR – preorbital process; PRF – parietal fossa; PSC – posterior semicircular canal; PT – postorbital process; RF – rostral fenestra; RN – rostral node; SC – supraorbital crest; SEF – subethmoid fossa; SF – stapedial foramen; SR – sphenopterotic ridge; SS – suborbital shelf. Illustration by L.J.V. Compagno.

margin, subterminal margin 2.1-2.4 in terminal margin. Dorsal caudal-fin margin proximally and distally convex, and mesially concave, without lateral undulations. Preventral margin basally straight or concave and apically convex, tip of ventral caudal-fin lobe narrowly rounded (young) or acutely pointed (adults), lower postventral margin concave, upper convex, notch between postventral margins forming angle of 80° (adults) to 125° (young), subterminal notch a narrow, deep slot, subterminal margin slightly concave, terminal margin slightly to strongly concave, lobe formed by these margins bluntly angular, and tip of tail narrowly rounded (young) to pointed (adults).

Vertebral counts and ratios listed for holotype and 9 paratypes in Table 4 and summarised as follows: total counts (TC) 158-167, precaudal (PC) counts 101-109, monospondylous precaudal (MP) centra 37-41, diplospondylous precaudal (DP) centra 63-69, diplospondylous caudal (DC) centra 55-60. MP counts 23.4-25.2%, DP counts 38.7-41.8%, and DC counts 34.7-36.6% of TC counts. Ratios of DP/MP counts 1.5-1.8, DC/MP counts 1.4-1.5, 'A' ratio 114.8-155.6, 'B' ratio 66.7-95.5. Transition between MP and DP centra over pelvic-fin bases and 1 or 2 centra behind pelvic-fin girdle. Last few MP centra before MP-DP transition moderately enlarged, not forming a 'stutter zone' of alternating long and short centra. Vertebra examined just behind cranium with strong wedge-shaped intermedialia and long diagonal calcified lamellae extending well into the basalia spaces.

Chondrocranium studied by dissection of an adult paratype (Fig.6A,C,E) and checked on radiographs of other specimens. Rostral cartilages elongated, slender, cylindrical, and not hypercalcified in adults. Medial rostral cartilage length 46% of nasobasal length (NBL), distance between bases of lateral rostral cartilages 1.9 in medial rostral cartilage. Medial rostral cartilage narrow-based, arched dorsally, lateral rostrals arched ventrally. Rostral node formed as a broad yoke with a large, anteriorly perforated rostral fenestra, separating the anterior end of the medial rostral cartilage from the lateral rostrals. Nasal capsules large, high, diagonally elliptical and somewhat wider than long, width across them 82% NBL, length of capsule 1.1 in its width. Anterior margins of nasal capsules nearly straight, slightly oblique to the cranial axis. Nasal apertures on ventrolateral faces of capsules, separated from large nasal fontanelles by a broad channel. Ectethmoid chambers inside nasal cavities, at posterior edges of nasal fontanelles and not visible ventrally. Subnasal plate in the form of irregular medial extensions of the lateral capsule wall, and broad lateral extensions of the narrow, high internasal septum bordering the wide nasal fontanelles. Strong ectethmoid condyles on posteroventral edges of nasal capsules, separated by a broad arcuate subnasal fenestra. Anterior fontanelle transversely oval, length about 1.2 times in its width and about 23% NBL. Dorsal lip of fontanelle not flared but with a prominent epiphysial notch. Cranial roof broadly arched, about level with supraorbital crests but not domelike. Parietal fossa deep. Orbital notches deep. Basal plate nearly flat from orbital notches to occipital centrum, without keels. Internal carotid foramina slightly closer to each other than to the stapedial foramina. Edge of supraorbital crests deeply arcuate in dorsal view, with short, prominent triangular Preorbital processes and laterally directed, ventrally hooked, bifurcated postorbital processes. Width across preorbital processes 71% NBL, width across postorbital processes 82% NBL, least width across supraorbital crests 2.0 in width across postorbital processes. Orbits horizontally subrectangular in lateral view, with contents indicated in Figure 6E. No ledge between suborbital shelves and nasal capsules. Suborbital shelves broadly convex, extending well lateral to the supraorbital crests in dorsal view. Width across suborbital shelves 69% NBL. Otic capsules not greatly expanded or inflated, their lengths about 25% NBL and greatest width across them 51% NBL. Sphenopterotic ridges diagonally arched in dorsal view, without a distinct Pterotic horn in lateral view. Opisthotic ridges high, extending laterally to edges of sphenopterotic ridges. Hyomandibular facets large, wedge-shaped, extending across rear half length of otic capsules and slightly exserted posteriorly. Occipital condyles broad and slightly exserted from occiput, with a single occipital centrum between them.

Intestinal valve with 7 (2 specimens) or 8 turns (3 specimens).

Colour. In alcohol adults are greyish brown above, lighter below, with prominent white-tipped dorsal, pectoral, pelvic and caudal fins (Fig.1). The tip of the terminal lobe of the caudal fin is dusky and the dorsal fins are abruptly dusky below their white tips, highlighting them. Young specimens below 400 mm TL have a series of solid dusky saddles on the back over the gills, pectoral-fin bases, first dorsal-fin base, interdorsal space, second dorsal-fin base, and caudal-fin base; also dark spots or bars over the eyes, on the flank just in front of the pelvic fin, and on the caudal-fin epichordal and terminal lobes. The dorsal-fin webs just below the white tips are more strikingly highlighted with blackish spots in juveniles than in adults.

Size. The largest known specimen of *H. falcata* is a 773 mm adult male. Of the ten specimens examined, one is an immature female, 258 mm, two are immature males, 251 to 380 mm, while seven are adult males, 695 to 773 mm. Weights of our specimens are given in Table 1.

Hemitriakis abdita n.sp.

Deepwater sicklefin houndshark

Fig.7

Type material. HOLOTYPE, CSIRO H1365-03, SO6/85/66, 596 mm adolescent male, 4 Dec. 1985, 17°38'S 150°11'E, Coral Sea Plateau off north-eastern Queensland, 225 m.

PARATYPES, CSIRO H1366-01, SO6/85/63, 360 mm immature male, 3 Dec. 1985, 17°30'S 149°41'E, Coral Sea Plateau off north-eastern Queensland, 401 m; CSIRO H1365-02, 536 mm immature female and CSIRO H1365-01, 465 mm immature male, SO6/85/66, 4 Dec. 1985, 17°38'S 150°11'E, Coral Sea Plateau off north-eastern Queensland, 225 m; CSIRO H1368-01, SO6/85/64, 561 mm immature female, 3 Dec. 1985, 17°30'S 149°46'E, Coral Sea Plateau off north-eastern Queensland, 343 m.

Diagnosis. *Hemitriakis* with eyes horizontally oval. Tooth rows 63-70 in both jaws. First dorsal-fin origin anterior to pectoral-fin free rear tips, over pectoral-fin insertions. First dorsal-fin length about 0.8-1.2 in distance from pectoral-fin free rear tips to pelvic-fin origins. Total vertebral counts 186-193, precaudal counts 126-130, monospondylous precaudal counts 48-53. Late juveniles and adolescents with prominent colour pattern of dark bars and saddles on body and fins. Males adolescent at 596 mm.

Etymology. From Latin *abditus*, hidden, in reference to the close external similarity of this sibling species to *H. falcata*.

Description. Proportional dimensions as percentage of total length (see terminology) for type series, listed in Table 2.

Head short, length 0.8-1.0 in pectoral-pelvic space; fairly narrow, flattened, roughly trapezodial in cross-section at eyes. Outline of head in lateral view nearly straight dorsally, slightly convex ventrally along lower jaws and nearly flat beneath gills; in dorsoventral view head anteriorly rounded and posteriorly tapering along branchial region. Preoral snout long, 1.2-1.3 in mouth width. Snout tip narrowly rounded in dorsoventral view, slightly indented anterior to nostrils; snout bluntly pointed in lateral view, nearly straight above and convex below.

External eye opening with prominent posterior notch but no anterior one; eyes large, elongate-oval in shape, eye length 5.1-6.5 in head length and 2.0-2.5 times eye height. Eyes dorsolateral on head, with lower edges well medial to horizontal head rim in dorsal view, subocular ridges prominent. Nictitating lower eyelids external, with deep but entirely scaled subocular pouches and secondary lower eyelids free from upper eyelids in young and adolescents.

Spiracles small, length 4.5-6.7 in eye length, spiracles 0.2 eye lengths behind and below posterior eye notch. First 4 gill openings about equally high or first slightly narrower than others; fifth shorter than third, height of fifth 0.6-0.7 of third; third 10.6-12.2 in head and 0.5-0.6 of eye length. All gill openings slightly concave, gill filaments not visible from outside. Upper ends of gill openings slightly below lower edges of eyes. Gill-raker papillae absent from gill arches.

Nostrils with large oval incurrent apertures lacking posterolateral keels, rounded anterior nasal flaps with

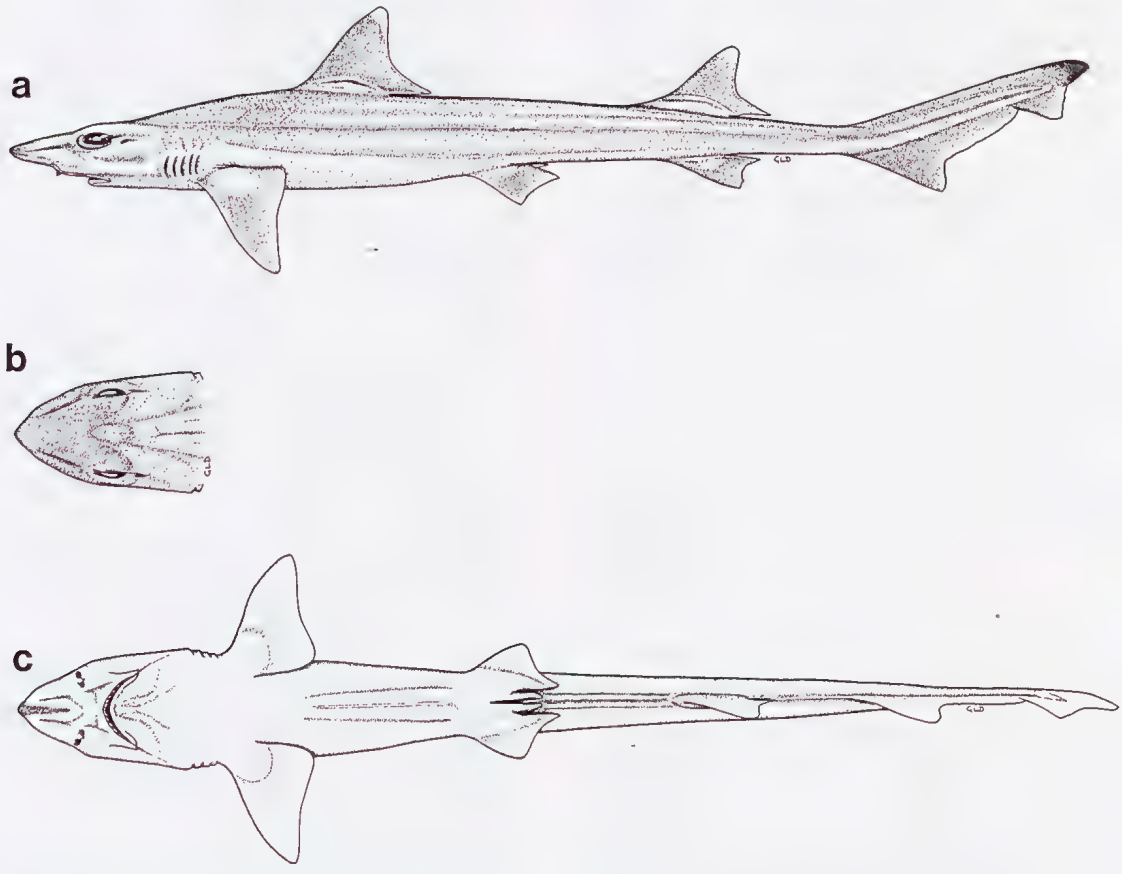

Fig.7. *Hemitriakis abdita* n.sp., holotype, H1365-03, 596 mm adolescent male, A, lateral and C, ventral views; B, dorsal view of head. Illustration by G. Davis.

round tips, elongated mesonarial flaps that prominently protrude from above the anterior nasal flaps, small oval excurrent apertures, and fairly large posterior nasal flaps. Nostrils well in front of mouth, about 3.1-3.5 times farther from snout tip than from eyes. Nostril width 1.9-2.4 in internarial space, 1.6-2.1 in eye length, 0.9-1.0 in third gill opening height.

Mouth broadly arched, moderately large, short, mouth width about 0.7 of head width at mouth corners, 2.9-3.3 in head length; mouth length 2.4-2.9 in mouth width. Tongue large, flat, broadly rounded, filling floor of mouth. Maxillary valve narrow, papillose. Palate and floor of mouth with tiny papillae, covered with buccopharyngeal denticles. Labial furrows long, upper 1.3-1.7 times lower furrows, anterior ends of uppers under first third of eye length and reaching virtually to symphysis of upper jaw. Labial cartilages large.

Teeth relatively few, in 34-37/28-33 rows (see Table 4 for detailed counts and statistics), 1-2/1-4 series functional. Teeth not arranged in diagonal files, no toothless spaces at symphysis. Tooth formulae:

$$\frac{\text{M5-6 AL11-13 P3-4}}{\text{M5 AL8-11 P3-5}} \quad \text{or} \quad \frac{\text{M5-6 AP14-17}}{\text{M5 AP11-14}}$$

Upper anterolateral teeth higher-crowned than lowers, both with well-developed distal cusplets and oblique cusps, cusps somewhat higher and more erect on upper teeth than lowers. Upper anterolateral teeth of immature and adolescent specimens examined with a strongly oblique cusp, a single cusplet, and a short blade. Medial teeth smaller than anterolaterals, with more erect cusps, higher crowns, and both mesial and distal cusplets. Anterolaterals gradually become lower crowned and lower-cusped along the dental band, grade into keel-like posterior teeth which are very low-crowned, lack cusps, and have a broad convex edge. All teeth have broad basal ledges, strong basal grooves, large mesial and distal root lobes separated by broad transverse grooves and prominent centrolingual foramen on linguobasal attachment surface of roots, medial teeth with lateral foramina. Transverse ridges obsolete on teeth of specimens examined, perhaps represented by irregular notching on basal ledge.

Body elongate, slender, trunk vertically oval to circular in section at first dorsal-fin base, length of trunk from fifth gill openings to vent 1.1-1.2 times head length. A low interdorsal ridge on midline of back between dorsal fins, and a low postdorsal ridge, but without predorsal ridges; lateral ridges absent from body. Caudal peduncle slender, cylindrical-tapering, without lateral keels or precaudal pits.

Lateral trunk denticles with elongated, teardrop-shaped crowns about 1.5 times as long as wide. Interspaces between ridges, including that between medial ridges, covered with reticulated depressions. Crown with prominent paired longitudinal ridges that diverge and then converge posteriorly to end at the medial cusps. Medial cusps relatively long and strong, a third to half length of crown. A pair of strong lateral ridges on crown, terminating in strong but short lateral cusps. Denticle crowns closely imbricated.

Pectoral fins narrow with broadly convex anterior margins, bluntly to acutely pointed apices, nearly straight (young) posterior margins, broadly rounded free rear tips, undulated to straight inner margins, narrow bases. Pectoral-fin anterior margin 1.3-1.5 times pectoral-fin length. Pectoral fins subequal in area to first dorsal fin. Origin of pectoral fins under fourth gill openings. Apex of pectoral fin posterior to its free rear tip when fin is elevated and adpressed to body.

Pectoral fin skeleton examined from radiographs, essentially similar to that of *H. falcata*. About 17-18 radials in 2 specimens that were countable, with 1 radial on propterygium, 5 on mesopterygium, approximately 11 on metapterygium (CSIRO H1365-01). Distal pectoral-fin radials with parallel edges and truncated tips, not pointed and tapering. Propterygium short, narrow, slightly elongated in the axis of its radial. Mesopterygium short, subangular, slightly expanded distally in the axes of its radials. Metapterygial basal segment triangular, elongated diagonal to the axes of its radials.

Pelvic fins broadly triangular. Pelvic-fin anterior margins 0.4-0.5 of pectoral-fin anterior margins; area subequal to anal-fin area. Pelvic-fin anterior margins slightly convex, apices narrowly rounded, posterior margin slightly concave, free rear tips pointed, inner margins straight. Claspers not examined in detail as there were no adult males in our sample.

First dorsal fin high, apically narrow and falcate, with basally concave and distally convex anterior margin, narrowly rounded apex, broadly concave posterior margin, acutely pointed free rear tip, nearly straight inner margin. First dorsal-fin origin slightly anterior to free rear tips of pectoral fins, midpoint of base varies from about equidistant between pectoral-fin insertions and pelvic-fin origins to 1.4 times closer to pectoral-fin insertions than pelvic-fin origins. First dorsal-fin insertion and free rear tip well anterior to pelvic-fin origins. Posterior margin slanting ventrally from apex, then abruptly posteriorly towards free rear tip, insertion about under level of dorsal apex. First dorsal-fin base 2.3-2.6 in interdorsal space, 2.2-2.5 in dorsal caudal-fin margin; first dorsal-fin height 1.1-1.3 in first dorsal-fin base; first dorsal-fin inner margin 2.0-2.3 in first dorsal-fin height, 2.1-2.9 in first dorsal-fin base.

Second dorsal fin high, apically narrow and falcate, nearly as large as first dorsal fin, second dorsal-fin height 0.7-0.8 in first dorsal-fin height, second dorsal-fin base 1.0-1.1 of first dorsal-fin base. Second dorsal fin with basally concave and apically nearly straight anterior margin, narrowly rounded apex, deeply concave posterior margin, acutely pointed free rear tip, straight or slightly concave inner margin. Second dorsal-fin origin separated from pelvic-fin insertions by a space about twice pelvic-fin base; free rear tip extending about level with anal-fin free rear tip but far in front of upper caudal-fin origin. Posterior margin extending ventrally from apex, then abruptly posteroventrally towards free rear tip, insertion about under dorsal apex. Second dorsal-fin

base 1.1-1.2 in dorsocaudal space, second dorsal-fin height 1.3-1.6 in second dorsal-fin base, second dorsal-fin inner margin 2.1-2.9 in second dorsal-fin height and 3.2-4.5 in second dorsal-fin base.

Anal fin low, apically narrow, semifalcate, much smaller than second dorsal fin, anal-fin height about 0.5 in second dorsal-fin height, anal-fin base 0.6-0.7 in second dorsal-fin base. Anterior margin concave basally and distally convex, apex bluntly rounded or sharply pointed, posterior margin deeply concave, free rear tip acutely pointed, and inner margin nearly straight. Anal-fin base with short preanal ridges, anal-fin origin behind second dorsal-fin origin by 0.2-0.3 of second dorsal-fin base, anal-fin insertion slightly behind or slightly in front of second dorsal-fin insertion. Anal-fin free rear tip well in front of lower caudal-fin origin. Anal-fin posterior margin slanting dorsally from apex, then abruptly posterodorsally towards free rear tip, anal-fin insertion about under apex. Anal-fin base 1.4-1.6 in anal-caudal space, anal-fin height 1.9-2.2 in anal-fin base, anal-fin inner margin 1.4-1.6 in anal-fin height and 2.7-3.4 in anal-fin base.

Caudal fin narrow-lobed, asymmetrical, with short terminal lobe and short but prominent ventral lobe. Caudal fin short, dorsal caudal-fin margin 3.6-3.8 in precaudal length. Preventral caudal-fin margin 2.3-2.4 and terminal lobe length 2.7-2.8 in dorsal caudal-fin margin, subterminal margin 1.5-2.4 in terminal margin. Dorsal caudal-fin margin proximally and distally convex, mesially concave, without lateral undulations. Preventral margin basally straight or concave, apically convex, tip of ventral caudal-fin lobe narrowly rounded or acutely pointed, lower postventral margin concave, upper convex, subterminal notch a narrow, deep slot, subterminal margin slightly concave, terminal margin slightly to strongly concave, lobe formed by these margins bluntly angular, tip of tail narrowly rounded or pointed.

Vertebral counts and ratios listed for holotype and 4 paratypes in Table 3 and summarised as follows: total counts (TC) 186-193, precaudal (PC) counts 126-130, monospondylous precaudal (MP) centra 48-53, diplospondylous precaudal (DP) centra 77-78, diplospondylous caudal (DC) centra 58-63. MP counts 25.8-27.5%, DP counts 39.9-41.9%, DC counts 31.0-32.8% of TC counts. Ratios of DP/MP counts 1.45-1.63, DC/MP counts 1.14, 1.27, 'A' ratio 115.0-133.3, 'B' ratio 53.5-70.5. Transition between MP and DP centra over pelvic-fin bases and 1-3 centra behind pelvic-fin girdle. Last few MP centra before MP-DP transition slightly enlarged, not forming a 'stutter zone' of alternating long and short centra.

Chondrocranium examined from radiographs of the type series, but these cannot be described in detail because of insufficient calcification of many cranial structures. Rostral cartilages elongated, slender, cylindrical, not hypercalcified in juveniles and adolescents. Medial rostral cartilage length about 59-63% of nasobasal length (NBL), distance between bases of lateral rostral cartilages 2.0-2.2 in medial rostral cartilage. Medial rostral cartilage narrow-based, arched dorsally. Rostral node formed as a broad yoke with a large, anteriorly perforated rostral fenestra. Nasal capsules large, high, diagonally elliptical, somewhat wider than long. Anterior margins of nasal capsules nearly straight, slightly oblique to cranial axis. Anterior fontanelle transversely oval, width about 29% NBL. Dorsal lip of fontanelle with a prominent epiphysial notch. Otic capsules not greatly expanded or inflated. Hyomandibular facets large, wedge-shaped, extending across rear half length of otic capsules and slightly exserted posteriorly. Occipital condyles broad and slightly exserted from occiput, with a single occipital centrum between them.

Intestinal valve with 7 (3 specimens) or 8 turns (2 specimens).

Colour. In alcohol juveniles and adolescents are greyish brown above, lighter below, with prominent white tips and posterior edging on the dorsal, pectoral and pelvic fins, and a white margin on the caudal fin below its terminal tip. There are a series of solid dusky saddles on the back over the gills, pectoral-fin bases, first dorsal-fin base, interdorsal space, second dorsal-fin base, and caudal-fin base; and dark spots or bars on the snout tip, on the underside of the snout, over and below the eyes, on the flank between the pectoral and pelvic-fin bases, and on the caudal-fin epichordal and hypochordal lobes. The base of the caudal-fin terminal lobe and the terminal tip is black. The dorsal-fin webs just below the white tips are strikingly marked with a pair of blackish bars.

Size. Of the five specimens of *H. abdita* examined, two are immature females, 536 and 561 mm, two are immature males, 360 to 465 mm, and the largest known specimen is a 596 mm adolescent male. Weights of our specimens are given in Table 2.

Distribution of *Hemitriakis abdita* and *H. falcata*. *Hemitriakis falcata* and *H. abdita* are allopatric as presently known (Fig.8). *Hemitriakis falcata* is known from the outer continental shelf of Western Australia from north-west of Dampier to north-west of Broome, at depths of 146 to 197 m. *Hemitriakis abdita* is only known from the southern Coral Sea Plateau south-east of Cairns on the north-eastern coast of Queensland, at depths of 225 to 401 m. At present there are no known records of the genus from intermediate localities. The known records are few but suggest that these two species may have depth habitat differences.

Comparisons between the Species of *Hemitraikis*

Compagno (1970, 1979, 1984, 1988) noted that *Hemitriakis* is readily distinguished from other triakid genera, but that the species of *Hemitriakis* are morphologically very similar in external appearance. Subtle differences in external morphology between these species are masked by inadequate series of specimens, by considerable growth changes in proportions and fin

and body shape between juveniles and adults (compare Figs 1 and 2), and by considerable variation within individuals of the same maturity class. There are few morphometric and external morphological characters that separate the species in our limited sample. Comparative morphometrics of *H. falcata*, *H. abdita*, *H. japanica*, and the New Caledonian *Hemitriakis* are presented in Tables 1 and 2.

Hemitriakis species have similar pectoral-fin radial counts with slight differences between species, but these differences are suspect with the small sample size presently available: *H. abdita* has about 17 to 18 radials, *H. falcata* 18 radials, *H. japanica* 19 radials, and *H. leucoperiptera* 17 radials. Intestinal valve counts are similar in *Hemitriakis* species and are probably not diagnostic: *H. abdita* and *H. falcata* have seven to eight intestinal valve turns, while *H. leucoperiptera* has seven turns and *H. japanica* six to eight turns (Compagno, 1988).

Hemitriakis species are most clearly separable by vertebral counts (Fig.9, Table 3), as are certain other triakids and some carcharhinids which are externally similar but differ sharply in numbers of vertebrae and in ratios of vertebral groups. Examples include sibling species of *Mustelus* in the Gulf of Mexico and the Gulf of California (Heemstra, 1973), sympatric species pairs within *Carcharhinus* such as *C. amboinensis* + *C. leucas* and *C. dussumieri* + *C. sealei* (Garrick, 1982), some allopatric species of *Rhizoprionodon* (Springer, 1964), and allopatric species of *Negaprion* (Compagno, 1988). There are also differences in colouration, in head and fin shapes, and in a few proportional dimensions between *Hemitriakis* species.

Hemitriakis falcata and *H. abdita* strongly differ from each other in precaudal vertebral counts (Fig.9), with no overlap between these taxa in MP, DP, PC and TC counts. There is an average difference in TC counts of about 27 centra between these species, and a separation of 19 centra between the highest *H. falcata* and lowest *H. abdita*. *Hemitriakis abdita* has the highest TC counts of any known *Hemitriakis*, but is approached by the New Caledonian *Hemitriakis* in total centra and is exceeded by it in PC and MP counts (see also Table 4). *Hemitriakis falcata* has MP, PC and TC counts broadly overlapping our sample of *H. japanica*, but averaging slightly higher TC counts and lower MP counts. *Hemitriakis leucoperiptera* in contrast has the lowest vertebral counts of any *Hemitriakis* and does not overlap any known species in precaudal counts. An undescribed species of *Hemitriakis* from the Philippine Islands was noted by Compagno (1970, 1979, 1984, 1988) to differ from the sympatric *H. leucoperiptera* in external morphology and colouration. This is represented by four fetal specimens in the Stanford University collections (SU-40097) which were left unnamed by Compagno (1988) because their vertebrae could not be counted and their teeth had not yet erupted. Re-examination of a radiograph of these specimens with high illumination and magnification revealed faint but barely countable precaudal centra on one of them. This has a count of MP 44, DP 72, and PC 116, which is much greater than comparable counts of *H. leucoperiptera* (Table 4) and is intermediate between *H. falcata* and *H. japonica* with lower MP and PC counts and *H. abdita* and the New Caledonian *Hemitriakis* with higher MP and PC counts (Fig.9).

Hemitriakis abdita differs from *H. falcata* in having a dusky bar on the ventral surface of the snout, and in narrower white tips to the dorsal fins.

Juvenile and early adolescent *H. abdita* and the New

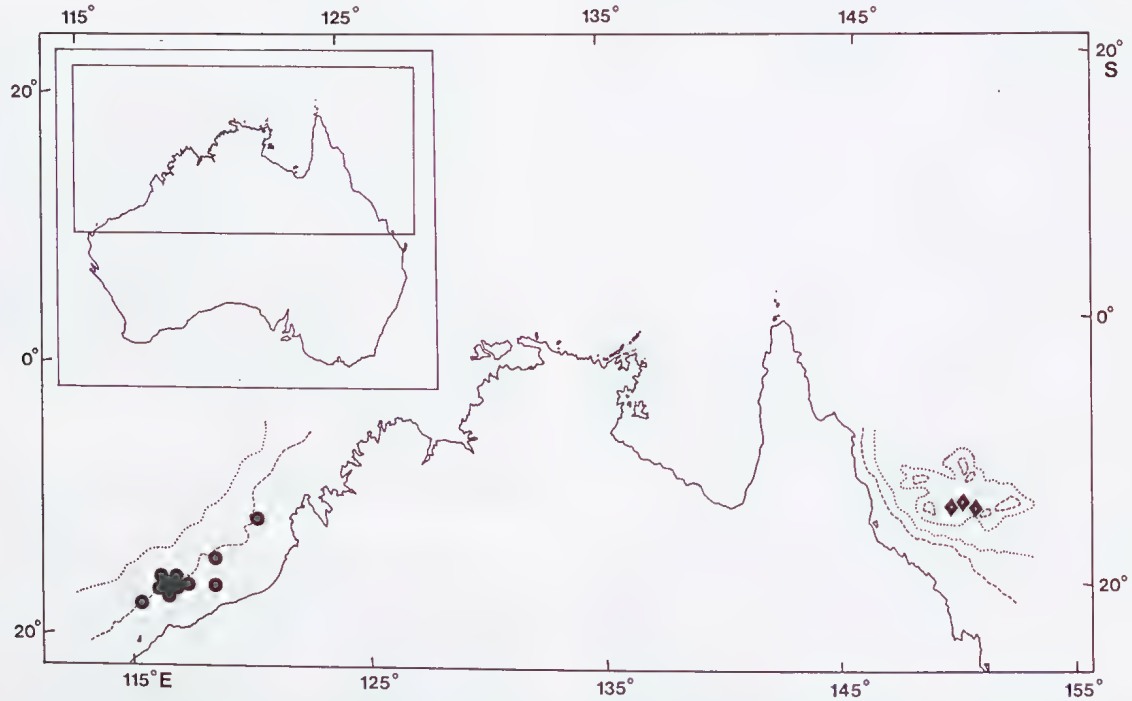

Fig.8. Map of northern Australia showing records of *Hemitriakis* spp. Inset map shows Australian continent with rectangle indicating area of main map. Diamonds – *H. abdita*; circles – *H. falcata*.

Caledonian *Hemitriakis* differ from *H. falcata* and *H. japanica* in having a slightly longer prenarial snout (PRN, Fig.10A, compare PRN in Tables 1 and 2). The greater PRN of *H. abdita* versus *H. falcata* is reflected in its longer rostral cartilages (see below). An adult female *H. leucoperiptera* as illustrated by Herre (1923: pl.1) agrees with large *H. japanica* males in having a broader head and more bluntly pointed snout than any of our (smaller) adult male *H. falcata*.

Similar-sized *H. falcata* and *H. japanica* differ in the flatter, more wedge-shaped head and slightly lower, more elongated, slitlike eyes of the latter species, which is also indicated by a plot of the ratio of eye length to eye height (EYL/EYH) versus total length for *Hemitriakis* species (Fig.10B). There is, however, considerable variation in EYL/EYH ratio for *H. japanica* and overlap with other species; the New Caledonian *Hemitriakis* has eyes which are as narrow as large *H. japanica*. The smaller eyes (and cranial orbits) of *H. japanica* may reflect its more inshore habitat compared to *H. falcata*.

Hemitriakis leucoperiptera agrees with *H. falcata*, *H. abdita* and the New Caledonian *Hemitriakis* in having falcate dorsal fins in adults or subadults and its first dorsal-fin origin in front of the free rear tips of the pectoral fin. *Hemitriakis japanica* has a more broadly angular dorsal, pectoral and anal fins, and the first dorsal-fin origin over or behind the free rear tips of the pectoral fin.

Hemitriakis abdita differs from *H. falcata* in having slightly higher tooth row counts, as shown on a plot of upper versus lower tooth row counts (Fig.10C). *Hemitriakis japanica* broadly overlaps these two species in tooth row counts (Table 3).

Young *Hemitriakis* are more boldly patterned than adults, as in many other carcharhinoid sharks (Compagno, 1988), but juvenile colour patterns differ between species. *Hemitriakis leucoperiptera* and *H. japanica* lack the bold spots and saddles of young *H. falcata*, *H. abdita* and the Philippine intermediate-count form. Young *H. japanica* have a dark upper caudal-fin terminal tip and young *H. leucoperiptera* have obscure saddles on their caudal peduncles and dusky epichordal caudal-fin lobes and terminal lobe bases (Compagno, 1988: fig.17.11A,B). Juvenile *H. abdita* differ from juvenile *H. falcata* in having a black snout tip and black bar on the underside of the snout and a dark bar beneath the eye. Late fetuses of the Philippine intermediate-count form have a dark spot on the snout tip and spots below the eyes as in *H. abdita*, but they differ from *H. abdita* and *H. falcata* in having light centers on their dark saddles and spots and a light rather than dark terminal caudal-fin tip (Compagno, 1988: fig.17.11C). The New

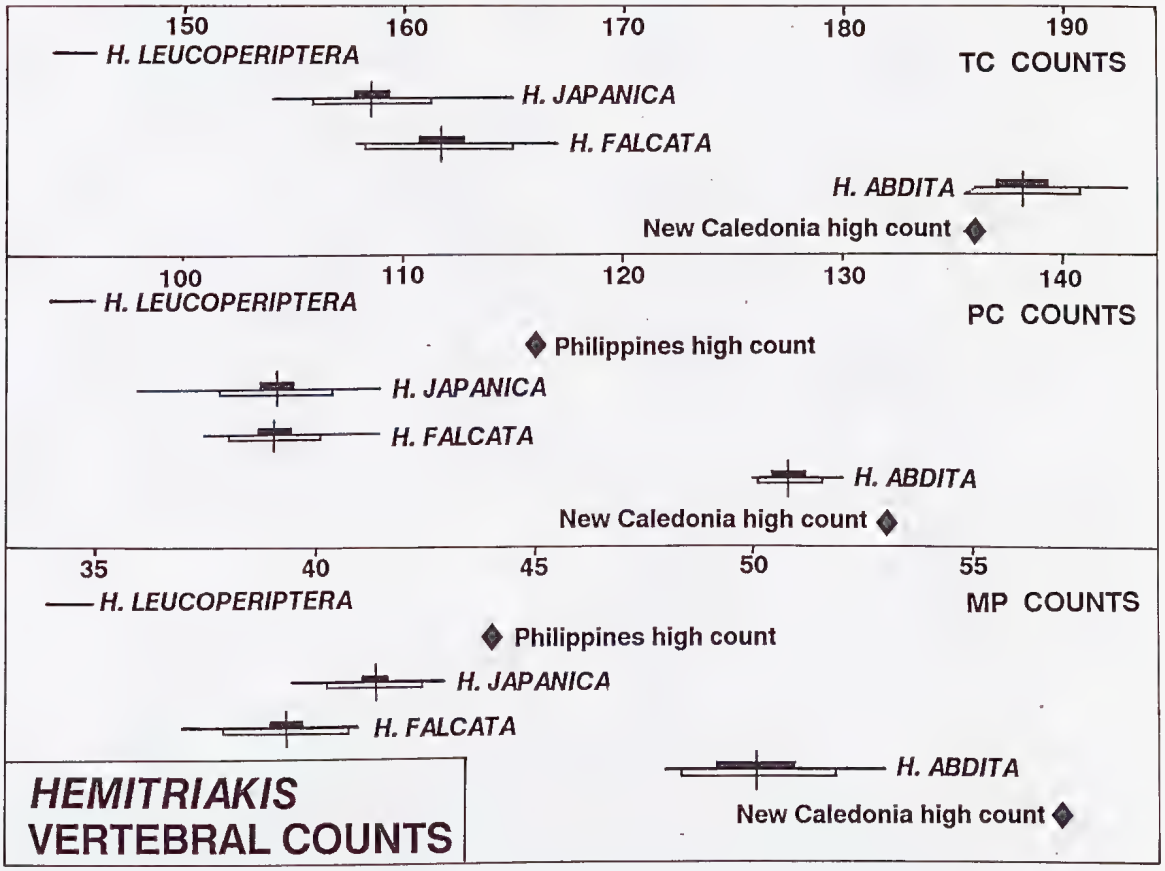

Fig.9. Horizontal line graphs of vertebral counts of *Hemitriakis* spp., including *abdita*, *falcata*, *japanica*, *leucoperiptera*, the undescribed Philippine high-count form, and the New Caledonian *Hemitriakis* near *abdita*. Horizontal line is range of counts, vertical line indicates arithmetic mean, solid bar above line is one standard error to either side of mean, hollow bar below line of mean is one standard deviation to either side of mean, diamonds indicate single counts. For detailed counts and statistics see Table 4.

Caledonian *Hemitriakis* (adult male) lacks dark bars and spots but has prominent white fin margins as in adults of *H falcata*, *H. japanica* and *H. leucoperiptera*.

The chondrocrania of *Hemitriakis falcata* (Fig.6A,C,E) and *H. japanica* (Fig.6B,D,F) are generally similar but differ in various details. The cranium of *H. japanica* has smaller, narrower, transverse nasal capsules with transverse anterior edges and smaller nasal fontanelles; smaller anterior fontanelle; cranial roof elevated above level of supraorbital crests in lateral view; less deeply

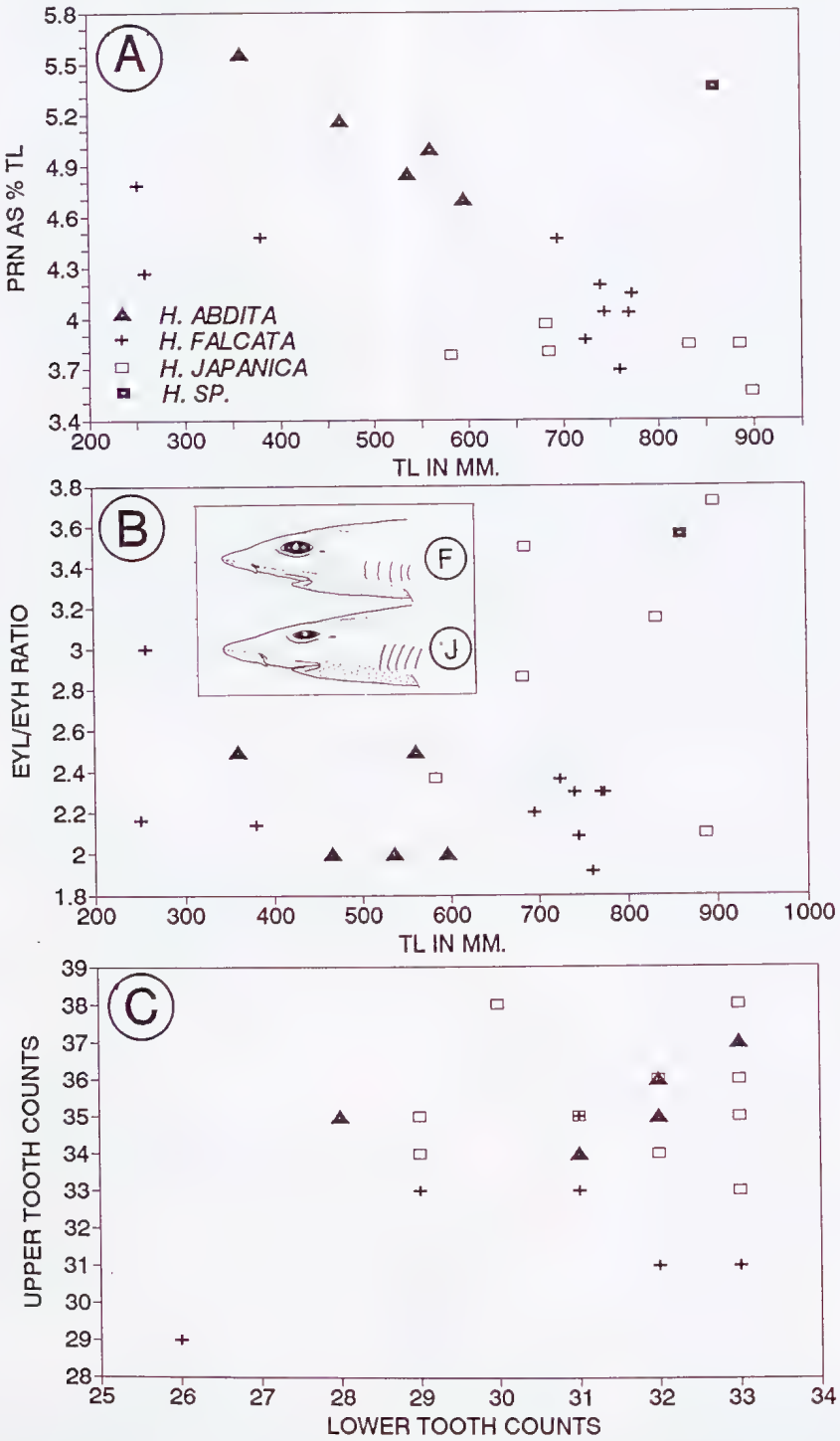

Fig.10. A = X-Y plot of prenarial length (PRN) as a percentage of total length versus total length (x-axis) for A – *Hemitriakis abdita*, F – *H. falcata*, J – *H. japanica*, N – *H. sp.* near *abdita* from New Caledonia. B = X-Y plot of eye length/height ratio (EYL/EYH) versus total length (x-axis) for A – *Hemitriakis abdita*, F – *H. falcata*, J – *H. japanica*, N – *H. sp.* near *abdita* from New Caledonia. Inset sketches of head in F – *H. falcata* (WAM P26271-001, 770 mm adult male holotype), J – *H. japanica* (LJVC-0421, 833 mm adolescent male), drawn to same scale, to show flatter head and lower, more slitlike eye of latter. C = X-Y plot of upper tooth row counts (y-axis) versus lower tooth row counts (x-axis) for A – *Hemitriakis abdita*, F – *H. falcata*. For detailed tooth row counts and statistics see Table 3.

concave supraorbital crest; lower, less ventrally-arching postorbital processes; more longitudinal sphenopterotic ridges; less laterally expanded suborbital shelves; narrower otic capsules. Differences between the crania of these two species mostly reflect the larger orbits of *H. falcata*. Comparison of the crania of *H. abdita* and *H. falcata* from radiographs suggest that the former species has a longer rostrum (medial rostral cartilage 59-63% of nasobasal length in 2 late juvenile specimens versus 45% in a dissected cranium of an adult *H. falcata*).

Male *Hemitriakis japanica* apparently mature at a larger size than *H. falcata* and may possibly grow larger. According to Chen & Mizue (1973) male *H. japanica* mature at about 850 mm and reach 1100 mm TL. However, a specimen of *H. japanica* from Taiwan was adult (or nearly so) at 675 mm (USNM 191193). Adults of *H. leucoperiptera* (adult female at 960 mm TL) and the New Caledonian *Hemitriakis* (adult male 860 mm TL) also attain a larger size than known *H. falcata* but maximum size is not known for any of these taxa and size at maturity is unknown for *H. leucoperiptera* and the New Caledonian *Hemitriakis*.

The taxonomic status of the New Caledonian *Hemitriakis* is somewhat problematical, but it is probably not conspecific with *H. leucoperiptera*, *H. japanica* and *H. falcata*. It is most similar to the geographically close *H. abdita* in general morphology and vertebral counts except for its slightly higher PC and MP counts and possibly narrower eyes. It may be conspecific with *H. abdita* and the few differences between it and *H. abdita* might be size-related and a result of our small sample. The largest *H. abdita* from the Coral Sea Plateau is a 596 mm adolescent male while the New Caledonian specimen is an 860 mm adult male. Until a wider series of *H. abdita* becomes available and direct comparison of *H. abdita* and New Caledonian material is possible we refer the New Caledonian specimen to *H.* sp. near *abdita* as a temporary expedient.

The Philippine high vertebral count *Hemitriakis* is still problematical because of its inadequate sample of four fetuses (SU 40097). The precaudal vertebral counts recorded here for one of these fetuses strengthens Compagno's (1988) suggestion that they represent an undescribed species of *Hemitriakis*.

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APPENDIX

Table 1. *Hemitriakis falcata* n.sp. Total lengths, weights and proportions as percent of total length for holotype and nine paratypes.

	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Coll. No.	WAM P 26271 -001	CSIRO CA 4056	WAM P 26274 -007	CSIRO H1094 -01	CSIRO H1035 -18	CSIRO H1035 -17	CSIRO H1035 -16	CSIRO H977 -9	CSIRO H1036 -27	CSIRO H1036 -26
SEX/M	M 4	M 2	F 2	M 2	M 4	M 4	M 4	M 4	M 4	M 4
WTgm	1024	44	36	141	695	724	740	744	760	773
TL mm	770	251	258	380	1150	1260	1100	1300	1350	1450
PCL	77.9	77.7	77.5	78.7	78.6	79.1	78.5	78.4	78.9	79.0
PRN	4.0	4.8	4.3	4.5	4.5	3.9	4.2	4.0	3.7	4.1
POR	6.6	8.8	7.8	7.6	7.3	6.8	6.6	6.6	6.4	6.7
POB	6.1	8.0	7.0	8.7	7.8	6.4	6.5	6.3	6.7	6.9
PSP	10.4	13.5	11.2	11.8	11.9	10.5	10.0	10.3	10.5	10.9
PGI	15.1	17.9	16.3	16.3	17.3	15.6	14.3	15.1	15.7	15.7
HDL	19.5	23.5	19.0	19.7	20.6	18.9	17.7	18.3	18.9	18.8
PP1	18.8	20.7	18.6	19.2	20.3	18.2	16.2	17.5	18.7	18.0
PP2	42.5	44.2	41.9	42.9	45.3	42.8	40.5	41.3	43.2	42.7
SVL	44.4	45.8	43.8	44.7	46.9	44.9	42.7	43.4	44.7	46.2
PAL	60.6	61.8	58.9	62.9	63.5	61.6	60.0	58.9	61.8	62.9
PD1	26.0	29.1	27.9	27.9	28.1	26.9	25.7	25.5	27.0	29.1
PD2	59.7	59.4	57.4	60.5	61.2	59.3	60.3	59.5	60.3	60.8
IDS	24.4	21.5	19.8	24.2	23.0	23.6	25.8	24.5	24.5	23.8
DCS	9.9	10.0	10.5	11.3	9.8	10.2	10.8	10.6	10.8	11.0
PPS	21.0	19.5	17.8	20.0	21.2	20.0	18.6	20.2	20.3	21.0
PAS	14.3	13.1	12.0	15.5	12.7	14.2	13.8	13.2	13.4	13.7
ACS	8.8	8.8	8.5	10.5	8.5	8.6	9.3	8.9	9.9	9.1
EYL	3.0	5.2	4.7	3.9	3.2	3.6	3.1	3.4	3.0	3.0
EYH	1.3	2.4	1.6	1.8	1.4	1.5	1.4	1.6	1.6	1.3
INO	6.8	8.8	7.4	7.4	6.9	7.3	6.8	7.5	6.1	6.1
NOW	1.4	2.4	1.6	1.8	1.7	1.7	1.4	1.6	1.7	1.6
INW	3.5	4.8	4.7	4.2	4.0	3.9	3.6	3.6	3.7	3.8
ANF	0.6	0.6	0.4	0.8	0.6	0.6	0.7	0.7	0.7	0.5
SPL	0.4	0.6	0.5	0.5	0.5	0.6	0.3	0.5	0.7	0.5
ESL	0.6	0.8	0.6	0.9	0.9	0.8	0.7	0.7	0.7	0.8
MOL	2.3	2.8	3.1	2.1	2.4	2.6	2.2	2.6	2.2	2.2
MOW	5.6	6.8	7.0	5.8	5.9	5.8	5.9	5.9	5.8	5.6
ULA	2.2	3.2	3.1	2.4	2.6	2.3	2.4	2.6	2.5	2.5
LLA	1.4	1.6	1.6	1.8	1.3	1.4	1.5	1.5	1.3	1.4
GS1	1.8	2.0	1.7	2.1	1.9	2.3	2.0	1.9	2.0	2.1
GS2	1.8	2.4	1.9	2.1	1.9	2.6	2.0	2.0	2.1	2.3
GS3	1.8	2.0	1.9	2.1	2.0	2.6	2.3	2.3	2.1	2.3
GS4	1.9	1.6	1.6	1.8	1.9	2.2	2.0	2.2	2.0	1.9
GS5	1.4	1.2	1.1	1.3	1.3	1.5	1.5	1.5	1.3	1.3
HDH	7.8	–	6.2	–	8.3	8.6	7.8	8.6	8.7	7.9
HDW	9.5	–	10.9	–	11.1	10.6	10.5	11.3	9.3	10.2
TRH	8.2	8.4	8.5	8.7	10.6	10.1	8.4	9.3	8.9	8.9
TRW	6.8	8.8	7.0	8.4	9.9	9.0	7.8	9.1	8.9	8.9
CPH	2.3	–	2.3	–	2.3	2.3	2.2	2.2	2.2	2.5
CPW	1.7	–	1.6	–	1.9	1.9	1.6	2.4	2.0	2.1
GIR	23.6	29.5	19.8	27.6	30.2	30.4	27.0	29.8	28.9	28.5
P1L	9.5	8.8	10.1	8.7	8.6	8.6	9.1	8.5	8.3	8.5
P1A	13.6	11.6	12.0	11.8	13.5	13.1	14.1	12.9	13.4	13.5
P1B	4.4	4.0	3.9	3.2	4.0	4.7	4.1	3.8	3.8	4.3
P1H	10.1	9.6	9.7	10.0	10.1	11.0	12.2	11.3	9.3	10.3
P1I	4.3	5.2	6.6	6.3	3.9	4.7	5.4	4.7	3.9	4.1
P1P	10.1	8.0	8.1	8.7	10.2	10.1	10.9	10.1	10.4	10.7
P2L	9.0	8.8	8.9	9.2	9.2	8.7	9.2	8.9	8.6	8.7
P2A	6.6	5.6	7.0	6.6	5.9	6.1	7.2	5.9	5.8	6.0
P2B	6.2	4.0	4.3	4.7	5.5	4.7	5.4	5.1	5.1	5.3

Table 1 (cont'd).

	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Coll. No.	WAM P 26271 -001	CSIRO CA 4056	WAM P 26274 -007	CSIRO H1094 -01	CSIRO H1035 -18	CSIRO H1035 -17	CSIRO H1035 -16	CSIRO H977 -9	CSIRO H1036 -27	CSIRO H1036 -26
P2H	3.6	2.8	3.9	3.2	4.9	4.1	3.5	4.0	3.8	4.1
P2I	2.7	4.8	3.9	4.2	4.0	3.3	3.0	2.6	3.7	3.5
P2P	4.7	4.8	3.9	4.2	5.0	5.1	4.5	5.4	4.5	4.9
CLO	6.5	1.6	–	2.4	6.0	7.3	7.4	7.3	7.1	6.6
CLI	10.1	5.6	–	5.3	10.5	10.9	11.2	10.9	10.9	10.9
CLB	1.4	0.8	–	0.8	1.4	1.4	1.4	1.2	1.2	1.3
D1L	14.2	12.4	12.4	13.4	14.7	13.8	13.4	14.0	13.9	14.4
D1A	13.0	10.4	11.6	11.8	13.4	13.0	13.0	13.2	12.4	13.3
D1B	10.0	9.2	8.9	9.5	10.4	10.1	9.2	10.2	10.0	10.5
D1H	6.1	6.4	7.0	8.4	7.8	8.1	7.7	8.5	8.4	8.3
D1I	4.2	4.0	3.9	4.2	4.7	3.9	4.3	3.9	4.6	4.1
D1P	7.1	6.0	8.5	7.1	7.8	9.5	9.5	9.4	9.1	9.4
D2L	12.9	12.4	12.0	11.3	12.8	13.1	12.3	12.5	11.7	12.2
D2A	12.1	10.0	10.9	10.3	11.4	11.7	11.4	11.6	10.4	10.9
D2B	9.2	8.4	8.9	8.4	9.2	9.5	8.8	9.3	8.2	8.9
D2H	6.4	4.8	5.4	6.3	6.2	6.4	6.4	6.5	5.9	6.0
D2I	3.5	2.8	3.1	3.7	3.6	3.6	3.9	3.2	3.6	3.2
D2P	6.0	4.8	5.8	5.8	6.9	7.2	6.2	7.1	6.6	6.2
ANL	10.3	9.2	9.7	7.9	9.4	9.3	9.9	10.5	8.8	9.3
ANA	8.8	8.4	8.1	6.3	8.3	8.1	8.6	–	7.8	7.5
ANB	7.1	7.2	7.0	5.5	6.8	6.5	8.5	8.9	6.3	6.7
ANH	3.9	2.8	2.7	3.2	3.5	3.7	3.4	3.8	3.7	3.4
ANI	2.5	2.8	2.7	2.6	2.9	2.6	2.7	–	2.5	2.5
ANP	6.0	3.2	3.5	2.9	3.7	3.6	3.9	–	3.2	3.8
CDM	21.4	20.3	21.3	21.6	21.3	20.9	21.2	21.5	20.5	20.6
CPV	11.2	9.2	9.3	9.5	10.2	9.8	10.7	9.1	10.1	10.1
CPL	2.5	1.2	1.9	2.1	2.7	2.6	2.2	3.1	2.8	2.6
CPU	2.1	7.6	7.8	9.5	8.1	8.1	7.8	8.2	8.8	8.0
CST	4.0	4.0	4.3	3.7	3.7	3.9	3.8	3.8	3.3	3.5
CTR	5.7	4.8	5.0	5.8	6.6	6.5	5.7	6.2	6.3	6.2
CTL	7.7	6.8	7.0	7.4	7.8	8.0	8.0	7.8	7.8	8.0
CFL	8.8	7.6	8.9	8.7	8.3	8.3	8.6	7.4	7.8	8.3
DPI	7.3	9.2	7.4	10.5	9.5	7.7	8.6	8.1	7.9	9.3
DPO	13.1	11.6	10.9	9.5	12.1	12.2	10.4	12.6	12.4	11.5
PDI	9.1	8.8	8.5	9.5	9.6	9.4	10.1	11.6	9.7	9.4
PDO	14.5	12.0	12.4	14.5	13.4	14.4	15.5	13.7	14.5	13.8
DAO	1.0	2.4	1.6	1.1	2.6	2.8	1.4	1.5	2.1	3.0
DAI	0.4	0.4	0.4	–	–	0.7	–	0.9	–	0.5
FOR	86.0	86.1	84.1	86.3	85.8	85.5	85.9	85.5	85.5	86.5

Table 2. *Hemitriakis* spp. Total lengths, weights and proportions as percent of total length for holotype and four paratypes of *H. abdita* n.sp., *Hemitriakis* sp. near *abdita* from New Caledonia (MNHN1986-720), and partial data for *H. japanica*.

	H. abdita					*H. sp*	*H. japanica*					
	Holotype	Paratype	Paratype	Paratype	Paratype							
Coll. No.	CSIRO H1365 -03	CSIRO H1366 -01	CSIRO H1365 -01	CSIRO H1365 -02	CSIRO H1368 -01	MNHN 1986-720	LACM SPA F422	SU 12677	USNM 191193	LJVC 0421	LJVC 0420	LJVC 0419
SEX/M	M 3	M 2	M 2+	F 2	F 2	M 4	F 2	F 2	F ?	M 3	M 4	M 4
WTgm	512	119	244	336	423	–	495	–	–	–	–	–
TL mm	596	360	465	536	561	860	582	682	685	833	886	898
PCL	78.2	78.3	78.3	77.4	78.4	83.7	78.4	–	–	–	–	–
PRN	4.7	5.6	5.2	4.9	5.0	5.3	3.8	4.0	3.8	3.8	3.8	3.6
POR	7.7	8.9	8.2	7.8	7.8	7.1	6.4	6.6	6.7	6.2	6.4	6.3
POB	7.4	8.9	8.0	8.0	7.5	7.7	6.7	–	–	6.4	6.2	6.5
PSP	11.2	13.1	11.8	11.8	11.6	11.6	10.7	–	–	9.6	9.8	10.0
PGI	16.3	17.5	16.6	16.8	16.4	17.8	15.8	–	–	14.8	15.8	14.6
HDL	19.6	21.4	20.9	20.5	20.0	22.2	19.6	19.6	20.0	18.2	19.2	18.7
PP1	19.0	20.8	20.2	20.0	19.4	19.7	17.7	–	–	17.4	18.3	17.8
PP2	41.9	42.2	42.8	42.0	41.2	43.6	42.1	–	–	–	–	–
SVL	43.1	44.4	44.5	44.0	43.7	47.1	44.7	52.1	45.8	–	–	–
PAL	59.1	59.2	60.6	60.1	61.1	66.3	60.7	–	–	–	–	–
PD1	25.5	28.3	27.7	26.1	27.6	29.3	27.0	–	–	–	–	–
PD2	57.2	58.9	58.1	57.1	57.8	56.2	58.6	–	–	–	–	–
IDS	22.5	22.5	22.8	22.0	23.0	24.8	21.8	–	–	–	–	–
DCS	11.2	10.6	10.8	10.8	12.1	10.0	10.5	–	–	–	–	–
PPS	19.8	16.7	17.2	19.4	19.3	18.6	21.1	–	–	–	–	–
PAS	14.8	13.9	13.5	12.7	13.4	15.0	14.1	–	–	–	–	–
ACS	9.9	9.7	9.2	10.1	9.8	8.7	8.2	–	–	–	–	–
EYL	3.0	4.2	3.4	3.4	3.6	3.7	3.3	2.9	3.1	2.6	2.4	2.9
EYH	1.5	1.7	1.7	1.7	1.4	1.0	1.4	1.0	0.9	0.8	1.1	0.8
INO	6.9	8.3	8.0	6.9	7.0	6.7	6.9	6.6	7.6	5.6	6.1	6.0
NOW	1.8	1.9	2.2	1.7	2.0	1.9	1.7	1.6	1.5	1.6	1.5	1.3
INW	3.9	4.7	4.1	3.9	3.7	4.1	3.6	3.8	3.8	3.4	3.6	3.6
ANF	0.7	0.6	0.4	0.4	0.7	0.6	0.5	–	–	0.6	–	0.6
SPL	0.7	0.7	0.6	0.6	0.5	0.4	0.7	0.6	0.6	0.6	0.5	0.7
ESL	0.7	0.8	0.6	0.6	0.7	0.7	0.7	–	–	0.8	–	0.8
MOL	2.3	2.8	2.4	2.4	2.5	3.4	2.6	2.8	2.6	2.3	2.6	2.7
MOW	5.9	7.5	6.9	6.3	6.1	6.9	6.4	6.2	6.0	5.5	5.8	6.9
ULA	2.3	2.8	2.8	2.2	2.5	2.6	2.2	2.5	2.3	2.2	2.3	2.7
LLA	1.5	1.7	1.9	1.7	1.8	2.1	1.4	1.5	1.8	1.4	1.6	1.8
GS1	1.8	2.2	2.2	1.9	1.6	2.1	2.1	2.1	2.3	2.2	2.5	2.3
GS2	1.8	2.2	2.4	1.7	1.6	2.3	2.2	–	–	2.4	2.5	2.4
GS3	1.8	1.9	1.9	1.7	1.8	2.2	2.1	2.1	2.3	2.4	2.5	2.4
GS4	1.8	1.7	1.7	1.5	1.6	1.9	1.9	–	–	2.2	2.1	2.2
GS5	1.2	1.1	1.3	1.1	1.2	1.3	1.9	1.8	2.0	1.7	1.5	1.7
HDH	–	–	–	–	–	6.6	7.4	4.0	3.8	4.7	3.7	5.2
HDW	–	–	–	–	–	10.7	9.8	8.5	8.3	8.6	7.8	9.6
TRH	8.4	8.9	7.5	7.8	9.3	–	8.8	8.2	7.2	8.0	7.1	9.0
TRW	7.9	8.3	8.2	8.0	7.1	–	8.6	10.0	8.5	9.4	9.5	9.8
CPH	–	–	–	–	–	2.9	2.6	–	–	–	–	–
CPW	–	–	–	–	–	1.9	1.9	–	–	–	–	–
GIR	27.2	26.4	24.9	24.3	27.1	–	27.7	–	–	–	–	–
P1L	8.9	8.6	8.6	8.6	8.4	10.6	8.4	10.0	9.9	8.5	8.5	8.5
P1A	11.9	12.2	11.8	12.9	12.3	14.4	10.8	13.2	13.4	13.3	12.0	12.6
P1B	5.0	3.9	4.7	4.7	4.3	4.2	4.0	–	–	4.4	4.1	3.9
P1H	11.2	11.1	11.2	11.6	11.6	14.3	9.1	–	–	10.8	–	10.1
P1I	4.4	5.8	4.9	5.0	5.2	6.4	4.3	–	–	4.3	4.6	4.1
P1P	10.2	10.0	9.9	10.4	10.0	12.6	8.2	–	–	9.2	–	10.5
P2L	8.7	8.9	8.6	8.6	8.6	9.4	8.6	–	–	8.6	–	8.4
P2A	5.9	5.6	6.0	6.2	5.3	6.3	6.2	5.9	6.1	6.5	–	6.0
P2B	5.0	5.0	4.7	4.7	4.5	4.5	5.5	–	–	5.3	–	–

Table 2 (cont'd).

	H. abdita					*H.* sp	*H. japanica*					
	Holotype	Paratype	Paratype	Paratype	Paratype							
Coll. No.	CSIRO H1365 -03	CSIRO H1366 -01	CSIRO H1365 -01	CSIRO H1365 -02	CSIRO H1368 -01	MNHN 1986-720	LACM SPA F422	SU 12677	USNM 191193	LJVC 0421	LJVC 0420	LJVC 0419
P2H	3.2	3.3	3.2	3.0	3.6	4.8	3.3	–	–	3.6	–	3.5
P2I	4.0	3.9	4.1	4.1	4.3	5.0	3.3	–	–	2.5	–	2.3
P2P	4.7	5.0	4.9	4.9	4.5	5.8	3.8	–	–	4.4	–	4.6
CLO	2.5	2.2	2.2	–	–	7.6	–	–	–	4.6	–	6.0
CLI	5.4	5.3	4.7	–	–	12.0	–	–	–	8.2	–	–
CLB	0.7	0.8	0.9	–	–	1.9	–	–	–	0.8	–	–
D1L	13.6	13.6	12.5	12.5	13.4	14.2	13.4	–	–	–	–	–
D1A	12.8	12.2	12.3	12.1	12.5	13.8	11.3	–	–	–	–	–
D1B	9.9	9.7	8.8	8.6	9.8	10.1	10.0	12.3	9.3	–	–	–
D1H	8.6	7.8	8.0	8.2	8.6	9.5	7.6	8.1	8.2	–	–	–
D1I	3.9	3.3	3.4	4.1	3.9	4.4	3.6	–	–	–	–	–
D1P	9.6	7.8	8.8	8.4	9.3	11.4	7.9	–	–	–	–	–
D2L	12.9	11.1	11.8	11.9	12.3	11.5	11.2	–	–	–	–	–
D2A	11.4	9.7	10.8	10.8	9.8	11.4	10.0	–	–	–	–	–
D2B	10.2	9.7	9.0	9.5	10.3	8.4	8.6	9.1	7.7	–	–	–
D2H	6.2	5.8	6.0	6.3	6.6	8.1	5.7	6.0	5.5	–	–	–
D2I	2.9	2.8	2.8	2.8	2.3	3.1	2.6	–	–	–	–	–
D2P	6.9	5.6	6.7	6.9	6.8	9.1	5.7	–	–	–	–	–
ANL	8.7	9.4	9.0	8.8	8.9	8.0	9.1	–	–	–	–	–
ANA	7.4	7.5	7.3	7.3	7.5	7.7	7.9	–	–	–	–	–
ANB	6.4	6.7	6.7	6.5	6.8	5.3	7.0	6.2	7.2	–	–	–
ANH	3.4	3.1	3.2	3.0	3.2	4.4	3.1	3.8	3.5	–	–	–
ANI	2.3	1.9	2.2	2.1	2.1	2.4	2.4	–	–	–	–	–
ANP	3.0	3.3	3.0	3.5	3.2	4.3	2.9	–	–	–	–	–
CDM	21.3	21.1	20.6	21.5	21.6	19.8	19.2	16.9	20.4	–	–	–
CPV	9.4	8.9	9.0	9.1	9.3	11.2	9.3	8.7	9.5	–	–	–
CPL	2.5	1.9	1.9	2.1	2.7	4.7	2.4	2.8	2.5	–	–	–
CPU	8.1	6.9	8.4	8.4	8.2	7.4	7.4	6.9	7.6	–	–	–
CST	4.0	4.2	3.7	4.1	4.1	4.1	4.0	3.7	3.8	–	–	–
CTR	5.5	5.8	6.2	6.2	6.4	6.5	5.2	6.5	7.0	–	–	–
CTL	7.7	7.5	7.5	7.8	8.0	7.9	7.6	7.8	8.0	–	–	–
CFL	9.1	8.6	8.2	8.6	8.7	8.8	7.9	–	–	–	–	–
DPI	8.7	6.7	8.4	7.8	10.9	5.8	11.2	10.4	10.7	–	–	–
DPO	12.1	10.3	9.9	12.3	8.6	12.8	10.3	11.3	11.7	–	–	–
PDI	8.2	7.5	8.2	8.8	9.3	9.9	8.9	9.7	9.2	–	–	–
PDO	13.9	13.9	14.6	12.9	13.0	12.8	14.4	12.2	13.0	–	–	–
DAO	3.4	1.9	1.9	2.8	2.5	2.2	2.1	3.2	0.9	–	–	–
DAI	–	–	–	–	1.1	–	0.7	0.7	1.0	–	–	–
FOR	86.1	86.1	85.6	85.1	85.4	–	85.6	–	–	–	–	–

Table 3. *Hemitriakis* spp., tooth row counts.

Hemitriakis japanica, Japan and Taiwan.

						Upper jaw			Lower jaw		
	Sex/M	T L	UT	LT	T T	AP	M	AP	AP	M	AP
USNM 191193	F	685	38	33	71	16	5	17	14	5	14
USNM 191193	M2	651	36	33	69	15	6	15	14	5	14
USNM 191193	M4	675	35	33	68	14	6	15	15	5	13
UMMZ-179060	M2	650	34	29	63	14	5	14	14	4	15
UMMZ-179061	F	560	36	32	68	15	5	16	14	4	14
UMMZ-179062	M2	505	33	33	66	15	1	18	13	1	15
SU-12677	F	682	35	29	64	16	5	15	12	5	12
LACM-F420	M2	350	34	32	66	15	4	15	13	5	14
LACM-F421	F2	582	36	32	68	15	5	16	13	5	14
LJVC-0419	M4	898	35	31	66	15	5	15	14	5	12
LJVC-0420	M4	886	38	30	68	16	5	17	12	5	13
LJVC-0421	M3	833	36	33	69	15	5	16	14	5	14
	range		33	29	63	14	1	14	12	1	12
			38	33	71	16	6	18	15	5	15
	mean		35.5	31.7	67.2	15.1	4.8	15.8	13.5	4.5	13.7
	SD		1.4	1.5	2.2	0.6	1.2	1.1	0.9	1.1	0.9
	SE		0.4	0.4	0.6	0.2	0.4	0.3	0.2	0.3	0.3
	CV		4.1	4.7	3.2	4.2	26.0	6.9	6.4	24.8	6.9
	N		12	12	12	12	12	12	12	12	12

Hemitriakis falcata, Western Australia

						Upper jaw			Lower jaw		
	Sex/M	T L	UT	LT	T T	AP	M	AP	AP	M	AP
WAM P76271-001	M4	770	35	31	66	15	5	15	13	5	13
WAM P76274-007	F2	600	31	33	64	14	5	12	14	5	14
CSIRO H1094-01	M2	380	31	32	63	14	4	13	14	4	14
CSIRO H1036-26	M4	773	29	26	55	13	3	13	12	3	11
CSIRO H977-01	M4	777	33	29	62	15	5	13	12	5	12
CSIRO H1036-27	M4	760	33	31	64	14	5	14	13	5	13
CSIRO H1035-18	M4	695	35	31	66	15	4	15	13	5	13
	range		29	26	55	13	3	12	12	3	11
			35	33	66	15	5	15	14	5	14
	mean		32.4	30.4	62.9	14.3	4.4	13.6	13.0	4.6	12.9
	SD		2.1	2.1	3.5	0.7	0.7	1.0	0.8	0.7	1.0
	SE		0.8	0.8	1.3	0.3	0.3	0.4	0.3	0.3	0.4
	CV		6.4	7.0	5.5	4.9	16.4	7.7	5.8	15.9	7.7
	N		7	7	7	7	7	7	7	7	7

Table 3 (cont'd).

Hemitriakis abdita, Queensland

	Sex/M	T L	UT	LT	T T	Upper jaw AP	M	AP	Lower jaw AP	M	AP
CSIRO H1365-01	M2	465	35	32	67	14	6	15	14	5	12
CSIRO H1365-02	F2	536	37	33	70	17	5	15	14	5	14
CSIRO H1365-03	M3	596	36	32	68	15	6	15	13	5	14
CSIRO H1366-01	M2	360	35	28	63	15	6	14	11	5	12
CSIRO H1368-01	F2	561	34	31	65	14	6	14	13	5	13
	range		34	28	63	14	5	14	11	5	12
			37	33	70	17	6	15	14	5	14
	mean		35.4	31.2	66.6	15.0	5.8	14.6	13.0	5.0	13.0
	SD		1.0	1.7	2.4	1.1	0.4	0.5	1.1	0.0	0.9
	SE		0.5	0.8	1.1	0.5	0.2	0.2	0.5	0.0	0.4
	CV		2.9	5.5	3.6	7.3	6.9	3.4	8.4	0.0	6.9
	N		5	5	5	5	5	5	5	5	5

Hemitriakis sp. near *abdita*, New Caledonia

	Sex/M	T L	UT	LT	T T	Upper jaw AP	M	AP	Lower jaw AP	M	AP
MNHN-1986-720	M4	860	35			17	1	17			

Table 4. *Hemitriakis* spp., vertebral counts and ratios.

Hemitriakis japanica, Japan and Taiwan.

	Sex/M	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU-12677	F2	682	42	65	52	107	159	26.4	40.9	32.7	1.5	1.2	122.9	66.2
UMMZ-179061	F2	560	43	63	54	106	160	26.9	39.4	33.8	1.5	1.3	132.1	71.2
UMMZ-179062	M2	505	42	62	52	104	156	26.9	39.7	33.3	1.5	1.2	94.6	77.8
UMMZ-179060	M2	650	41	65	53	106	159	25.8	40.9	33.3	1.6	1.3	128.2	75.8
USNM-191113	F2?	685	41	63	56	104	160	25.6	39.4	35.0	1.5	1.4	119.6	84.6
USNM-191113	M2	651	41	66	54	107	161	25.5	41.0	33.5	1.6	1.3	121.6	75.0
USNM-191113	M4	675	41	62	56	103	159	25.8	39.0	35.2	1.5	1.4	107.7	71.2
LACM F-421	F2	582	43	62	52	105	157	27.4	39.5	33.1	1.4	1.2	123.5	91.3
LACM F-422	F2	350	41	63	54	104	158	25.9	39.9	34.2	1.5	1.3	133.3	88.9
CAS-1971:VII-16	F2	231	41	61	56	102	158	25.9	38.6	35.4	1.5	1.4	144.4	76.5
CAS-1971:VII-22	F2	219	43	66	56	109	165	26.1	40.0	33.9	1.5	1.3	162.5	81.3
CAS-28576	F2	353	42	56	56	98	154	27.3	36.4	36.4	1.3	1.3	82.1	76.7
CAS-28576	M2	307	39	63	53	102	155	25.2	40.6	34.2	1.6	1.4	123.5	87.5
CAS-28576	M2	252	40	63	56	103	159	25.2	39.6	35.2	1.6	1.4	125.0	71.4
	range		39	56	52	98	154	25.2	36.4	32.7	1.3	1.2	82.1	66.2
			43	66	56	109	165	27.4	41.0	36.4	1.6	1.4	162.5	91.3
	mean		41.4	62.9	54.3	104.3	158.6	26.1	39.6	34.2	1.5	1.3	122.9	78.2
	S		1.1	2.4	1.6	2.6	2.6	0.7	1.1	1.0	0.1	0.1	18.8	7.2
	SE		0.3	0.6	0.4	0.7	0.7	0.2	0.3	0.3	0.0	0.0	5.0	1.9
	CV		2.7	3.8	3.0	2.5	1.6	2.7	2.9	3.0	4.8	4.3	15.3	9.3
	N		14	14	14	14	14	14	14	14	14	14	14	14

Hemitriakis leucoperiptera, Philippines

	Sex/M	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU-27118	M2	169	34	62	50	96	146	23.3	42.5	34.2	1.8	1.5	216.7	118.2
SU-27118	F2	170	35	59	50	94	144	24.3	41.0	34.7	1.7	1.4	137.5	100.0

Hemitriakis n.sp., Philippines

	Sex/M	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
SU-40097[3]	F1	161	44	72	–	116	–	–	–	–	1.6	–	–	–

Table 4 (cont'd).

Hemitriakis falcata, Western Australia

	Sex/M	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
WAM-P26271-001	M4	770	41	64	58	105	163	25.2	39.3	35.6	1.6	1.4	123.9	73.1
WAM-P26724-007	F2	258	41	64	60	105	165	24.8	38.8	36.4	1.6	1.5	146.2	86.4
CSIRO H1036.26	M4	773	38	65	55	103	158	24.1	41.1	34.8	1.7	1.4	150.0	93.5
CSIRO H1035.17	M4	724	37	66	55	103	158	23.4	41.8	34.8	1.8	1.5	114.8	75.6
CSIRO H977.01	M4	744	41	63	59	104	163	25.2	38.7	36.2	1.5	1.4	134.1	80.8
CSIRO H1035.16	M4	740	40	69	58	109	167	24.0	41.3	34.7	1.7	1.5	133.3	95.5
CSIRO H1036.27	M4	760	39	67	57	106	163	23.9	41.1	35.0	1.7	1.5	145.7	93.1
CSIRO H1035.18	M4	695	39	63	56	102	158	24.7	39.9	35.4	1.6	1.4	133.3	83.3
CSIRO H1904.01	M2	380	40	64	60	104	164	24.4	39.0	36.6	1.6	1.5	133.3	66.7
CSIRO CA4056	M2	251	38	63	58	101	159	23.9	39.6	36.5	1.7	1.5	155.6	70.0
	range		37	63	55	101	158	23.4	38.7	34.7	1.5	1.4	114.8	66.7
			41	69	60	109	167	25.2	41.8	36.6	1.8	1.5	155.6	95.5
	mean		39.4	64.8	57.6	104.2	161.8	24.3	40.1	35.6	1.6	1.5	137.0	81.8
	S		1.4	1.9	1.7	2.1	3.1	0.6	1.1	0.7	0.1	0.0	11.8	9.8
	SE		0.4	0.6	0.6	0.7	1.0	0.2	0.4	0.2	0.0	0.0	3.7	3.1
	CV		3.4	2.9	3.0	2.0	1.9	2.3	2.8	2.0	4.9	2.2	8.6	12.0
	N		10	10	10	10	10	10	10	10	10	10	10	10

Hemitriakis abdita, Queensland

	Sex/M	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
CSIRO H1365.03	M3	596	51	78	58	129	187	27.3	41.7	31.0	1.5	1.1	124.0	68.9
CSIRO H1368.01	F2	561	53	77	63	130	193	27.5	39.9	32.6	1.5	1.2	115.0	53.5
CSIRO H1365.01	M2	465	49	77	60	126	186	26.3	41.4	32.3	1.6	1.2	133.3	70.6
CSIRO H1366.01	M2	360	48	78	60	126	186	25.8	41.9	32.3	1.6	1.3	125.0	55.6
CSIRO H1365.02	F2	536	49	78	62	127	189	25.9	41.3	32.8	1.6	1.3	127.3	66.7
	range		48	77	58	126	186	25.8	39.9	31.0	1.5	1.1	115.0	53.5
			53	78	63	130	193	27.5	41.9	32.8	1.6	1.3	133.3	70.6
	mean		50.0	77.6	60.6	127.6	188.2	26.6	41.2	32.2	1.6	1.2	124.9	63.0
	S		1.8	0.5	1.7	1.6	2.6	0.7	0.7	0.6	0.1	0.0	5.9	7.1
	SE		0.8	0.2	0.8	0.7	1.2	0.3	0.3	0.3	0.0	0.0	2.7	3.2
	CV		3.6	0.6	2.9	1.3	1.4	2.6	1.7	1.9	3.8	3.8	4.7	11.3
	N		5	5	5	5	5	5	5	5	5	5	5	5

Hemitriakis sp. near *abdita*, New Caledonia

	Sex/M	T L	MP	DP	DC	PC	TC	%MP	%DP	%DC	DP/MP	DC/MP	A	B
MNHN-1986-720	M4	860	57	75	54	132	186	30.6	40.3	29.0	1.3	0.9	121.7	74.7

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Review of the Upside-down Flies (Diptera: Neurochaetidae) of Madagascar and Africa, and Evolution of Neurochaetid Host Plant Associations

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ABSTRACT. The subgenera *Neurocytta* McAlpine and *Neurotexis* McAlpine are raised to genera. A revised key to genera of recent Neurochaetidae and a key to species of *Neurotexis* are given. The new species *Neurotexis maura, N. despiciens, N. termon, N. kaplanae, N. delphis, N. charis, N. primula, N. vesca, N. freidbergi* and *N. polyaster*, all from Madagascar, are described. *Neurocytta prisca* (McAlpine) and *Neurotexis stuckenbergi* (McAlpine) are new combinations (from *Neurochaeta*). Additional morphological details are given for *Neurocytta prisca*. Morphology of the neurochaetid antenna is reviewed. Head-downwards cursorial behaviour is recorded for almost all known Afrotropical species. Apparent host plants recorded for 11 of these are *Strelitzia* and *Ravenala* (Zingiberales: Strelitziaceae) and *Pandanus* (Pandanales: Pandanaceae). Host plant records are superimposed on a revised cladogram of neurochaetid species in an attempt to trace out evolutionary changes in fly-plant associations. An early zingiberalean plant possibly provided the plesiotypic host plant association for Neurochaetidae, and there is evidence that such a plant may have been available to the early Tertiary neurochaetid *Anthoclusia*.

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The family Neurochaetidae has been only recently described (McAlpine, 1978) and, when the family was last revised (McAlpine, 1988a, 1988b), the Afrotropical representatives were still only known from three preserved specimens. Significant new material was obtained through recent field work in Madagascar and Zimbabwe by A. Freidberg, F. Kaplan, and the author. It is probable that additional Afrotropical species await discovery, but with more than 300 specimens available, I am able to record a significant increase in knowledge of the fauna.

Previously (McAlpine, 1988a) I separated the two imperfectly known Afrotropical species as two monotypic subgenera of *Neurochaeta* McAlpine, preferring caution in view of the slight knowledge of this fauna. With the ten new species here described, it is clear that the Madagascar species form a well-defined monophyletic group with some diversity, comparable with *Neurochaeta* s.str. of the Oriental and Australian regions, also that the only known African species is phylogenetically removed from both the above groups.

The forecast of Woodley (1982) that separate genera (from *Neurochaeta*) might eventually be needed for *N. prisca* and *N. stuckenbergi* is now fulfilled, *Neurocytta* McAlpine and *Neurotexis* McAlpine being elevated to generic status.

The head-downwards cursorial behaviour responsible for the appellation 'upside-down fly', has been shown to be general for *Neurochaeta* s.str. (McAlpine, 1988b), but new observations demonstrate its presence also in species of *Neurocytta* and *Neurotexis*. The similarity of *Neurocytta* to the Tertiary stem-group *Anthoclusia* Hennig suggests that the latter may have possessed similar cursorial behaviour.

Morphological terminology here follows that of Harrison (1959) with particular morphology for Neurochaetidae as given by McAlpine (1988a).

The names of the following collectors are abbreviated to the initials: A. Freidberg, F. Kaplan, D.K. McAlpine.

Institutions housing specimens are abbreviated as follows: AM – Australian Museum, Sydney; BM – British Museum (Natural History), London; CNC – Canadian National Collection, Agriculture Canada, Ottawa; MNM – Hungarian National Museum, Budapest; NAT – Natal Museum, Pietermaritzburg; PM – National Museum of Natural History, Paris; TAU – George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv; USNM – National Museum of Natural History, Washington.

Key to Recent Genera of Neurochaetidae

1. Eye with coarse ommatrichia; costa unbroken; alula without fringe; functional tarsal claws absent (Australia) ..... *Nothoasteia*

—— Eye with at most few, minute ommatrichia; costa with break at end of subcosta; alula with marginal fringe; tarsal claws developed 2

2. Arista short-plumose, its longer rays less than 0.2 length of arista; scutellar bristles of major pair approximated near apex; subscutellum little developed (Fig.1B); second basal cell complete (Africa) ..... *Neurocytta*

—— Arista long-plumose, its longer rays more than 0.3 length of arista; scutellar bristles of major pair widely separated; subscutellum enlarged, encroaching on postscutellum (Fig.1C); second basal cell incomplete 3

3. Second basal cell confluent with discal cell; costa terminating at vein 3; radial sector without bristles; posterior margin of scutellum bare between major bristles (Madagascar) ..... *Neurotexis*

—— Second basal cell confluent with first basal cell; costa terminating at vein 4; radial sector dorsally towards base with 2-4 strong erect bristles; posterior margin of scutellum with one or more pairs of shorter bristles between major pair (South East Asia to Australia) ..... *Neurochaeta*

Neurocytta McAlpine n.stat.

Neurocytta McAlpine 1988a: 43, 44 (as subgenus of *Neurochaeta*). Type species *Neurochaeta prisca* McAlpine.

Comments. This group remains monotypic and, though the diagnostic characters given previously are still valid, the frontal bristles and antennae of the previously available material were damaged. The following is a supplement to the previous subgeneric description on the basis of additional specimens.

Description. Fronto-orbital bristles 4, including 2 reclinate bristles (1 specimen with anterior reclinate bristle duplicated on both sides) and, anteriorly, 2 incurved bristles, 1 situated mesad of and slightly in advance of foremost reclinate bristle, and 1 situated well in advance of and somewhat less mesad of anterior reclinate bristle. Antennal segment 2 less enlarged and cucullate than in *Neurotexis* and *Neurochaeta*, with comb of setulae on outer distal margin very weakly developed, without a differentiated ventral bristle; arista with well developed, rotund, short-haired segment 5; segment 6 bipectinate, with rays no longer than diameter of segment 5. Prosternum oblong, with median groove and several marginal setulae on each side; metasternum setulose; scutellum and postscutellar parts, other than subscutellar

membrane, strongly dorsoventrally compressed; subscutellum little developed, narrowed medially, not encroaching on the much deeper postscutellum.

Notes. I have previously (McAlpine, 1978, 1988a) mentioned several characters in which *Neurocytta prisca* resembles the Baltic amber fossil *Anthoclusia* Hennig (particularly *A. gephyrea* Hennig) rather than the other recent species of *Neurotexis* and *Neurochaeta*. Observations on the new material of *Neurocytta* confirm the plesiomorphic proportions of the subscutellum and postscutellum which would appear to resemble those of *Anthoclusia*, though both parts are reduced in depth in *Neurocytta*. The presence of two pairs of inclinate fronto-orbital bristles in *Neurocytta* is also in agreement with *Anthoclusia* (see particularly Hennig 1967), though in *Neurocytta* these are situated mesad of the line of the reclinate fronto-orbitals as in *Neurotexis* and *Neurochaeta*. The antenna of *Neurocytta* resembles that of *Anthoclusia* and differs from that of *Neurotexis* and *Neurochaeta* in having a less developed segment 2 without a differentiated ventral bristle, and in having the arista (segment 6) with relatively numerous quite short dorsal and ventral rays. *Anthoclusia remotinervis* Hennig differs from *A. gephyrea* Hennig in having the lateral scutellar bristle replaced by two or three small setulae ("Härchen"), a condition approaching that of *Neurocytta*. *Neurocytta* also agrees with *Anthoclusia* and differs from some other living neurochaetids in the presence of a distal anteroventral comb on the fore femur.

While I do not believe that there is adequate evidence to demonstrate that the known species of *Anthoclusia* can be assigned to separate lineages ancestral to various living neurochaetids, it is interesting to note that some of the present diversity of modern neurochaetids was represented in this early Tertiary fauna. The supplementary observations on *Neurocytta*, given above, confirm its status as an interesting link between the fossil forms of *Anthoclusia* and the living *Neurochaeta* and *Neurotexis*.

Neurocytta prisca (McAlpine) n.comb.

Figs 1, 8

Neurochaeta prisca McAlpine, 1978: 282-283, figs 9-11, 21.

Additional material examined. 4 females, 'Banana Grove', Chimanimani (formerly Melsetter) National Park, 23 Sept. 1990, D.K.M. (AM, USNM).

Distribution. Zimbabwe (formerly Southern Rhodesia) – mountains of eastern border district. The distribution is probably limited by availability of *Strelitzia* plants. The type locality is given as 'Melsetter', a village now called Chimanimani. *Strelitzia augusta* grows in the vicinity of Bridal Veil falls, about 3 km from the village. This may be the source of the type material, but, in my brief visit there, I did not find *N. prisca*. 'Banana Grove', where I collected my material, is about 22 km further east.

Notes. The previously given characterisation of the species is supplemented under the generic heading.

Neurotexis McAlpine n.stat.

Neurotexis McAlpine 1988a: 43, 44 (as subgenus of *Neurochaeta*). Type species *Neurochaeta stuckenbergi* McAlpine.

Comments. The diagnostic characters are essentially as given by me (1988a) for the monotypic subgenus *Neurotexis*, but, because several species have now been seen, the description must be modified.

Description. Fronto-orbital bristles normally 4, the inclinate one inserted mesad of and somewhat before to somewhat behind anterior reclinate one; postvertical

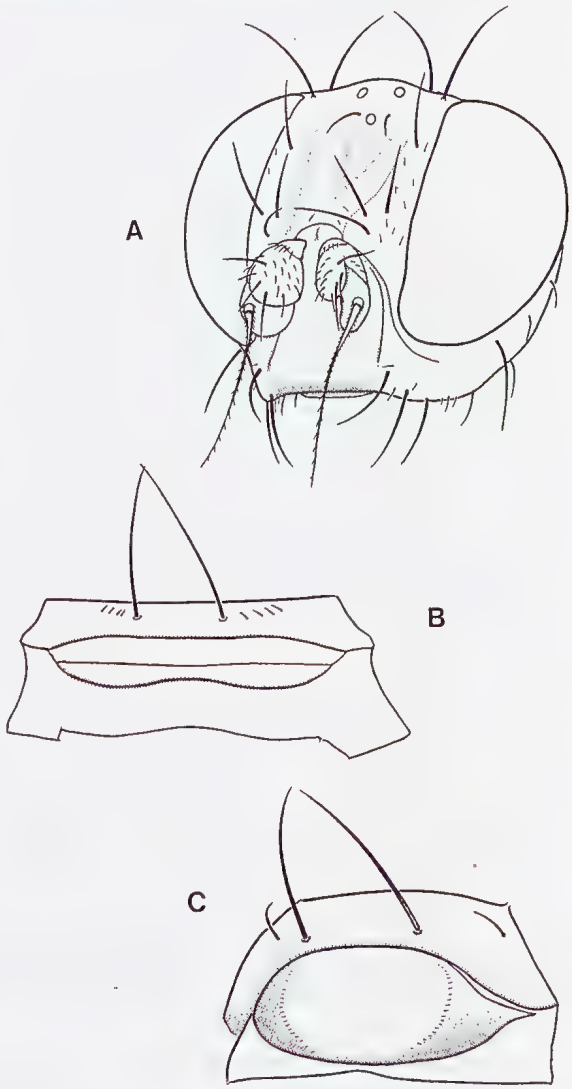

Fig.1. *Neurocytta prisca*. A, head; B, scutellum and postscutellar parts posterior aspect. *Neurotexis primula*: C, same parts.

bristle and one postgenal bristle present; suborbital bristle absent. Antenna: segment 2 large and cucullate, with ventral bristle usually long, its medial lobe with several thick bristles, outer lobe with a regular marginal series of pale setulae; segment 3 with group of enlarged apical microtrichia; segments 4 and 5 very small, pubescent, sclerotised; segment 6 long-plumose, with several long dorsal rays situated on basal swelling, beyond base with long dorsal and ventral and short medial rays. Presutural bristle present, sometimes vestigial; dorsocentral bristles 1 or 2; supra-alar bristles 1 or 2; scutellar bristles in 2 pairs: widely separated major pair, and shorter lateral pair; subscutellum deep, convexly prominent, usually with silvery pruinescent zone; mesopleuron devoid of setulae; sternopleuron with 1 or 2 upper posterior bristles, with or without short upper anterior bristles; prosternum and metasternum bare. Costa terminating immediately beyond end of vein 3, with spaced anteroventral bristles between terminations of veins 1 and 2, without erect dorsal setulae immediately before end of subcosta; costal section before subcostal break produced distally in front of break as a long, finger-like process (costal lappet), or only vestigial process present; radial sector without macrotrichia; distal section of vein 5 not shorter than penultimate section of vein 4; second basal cell separate from first basal cell, confluent with discal cell; anal cell small, often imperfectly enclosed; vein 6 often sclerotised for short distance beyond anal cell; alula rather narrow. Abdominal tergites 2 or 3 to 6 or 7 with bristle near each posterolateral angle. Postabdomen of male, where known, with well developed, asymmetrical sternites 6 and 7, and dorsal sternite 8; epandrium well developed, with 2 pairs of long bristles and articulated surstylus, which is not expanded into a basal plate; hypandrium with pair of large, almost flat plates each having 1 or 2 bristles, without process (outer gonite of McAlpine, 1988a) at lateral margin of each plate (present in *Neurochaeta* s.str.), but with well-developed, bristled posterior gonite (corresponding to inner gonite of *Neurochaeta*); basiphallus rather short, sclerotised, with strong posterior process (epiphallus); distiphallus long, coiled in repose like a watch spring, sclerotised only on 2 longitudinal strips; proctiger with pair of ridges, each with sclerotised strip along summit.

Notes. The presence of two posterior sternopleural bristles in some species of *Neurotexis* prevents the number of sternopleurals being used as an apomorphy in evidence for uniting *Neurotexis* and *Neurochaeta* as a monophyletic group (see Woodley, 1982; McAlpine, 1988a). However, this monophyly is further supported by the following apparent synapomorphies: antennal segment 2 enlarged; antennal segment 2 with one enlarged ventral bristle; rays of arista lengthened and reduced in number; subscutellum with shining silvery pruinescence.

Two features of the epandrium of male *Neurotexis* are highly characteristic and probably ground plan states for the genus, though they cannot be classed as autapomorphies for *Neurotexis* on present evidence. These are: epandrium with two pairs of enlarged bristles, and epandrium with zone of silvery pruinescence. In *Neurochaeta*, the sister group of *Neurotexis*, the greatly reduced epandrium (an autapomorphy for *Neurochaeta*) has, in some species, one or two pairs of bristles, so that an ancestral form may have shared the epandrial bristling occurring in *Neurotexis*. In view of the great reduction of the epandrium in *Neurochaeta*, any pruinescent zone, which an ancestor might have shared with ancestral *Neurotexis*, would probably have been lost.

The following distinctive apomorphies attest to the monophyly of the genus *Neurotexis* in its newly expanded scope: i) presutural bristle present; ii) costa terminating just beyond vein 3; iii) distal section of vein 4 largely desclerotised; iv) dorsal macrotrichia on radial sector absent; v) second basal cell confluent with discal cell.

Like *Neurochaeta* s.str., *Neurotexis* is now known to exhibit some morphological diversity. The two groupings shown in couplet 1 of the key to species and in Figure 9 are perhaps monophyletic. The *polyaster* group (*N. vesca, N. freidbergi, N. polyaster*) shows the following possible autapomorphies: frontal bristles shortened; scutellum shortened; 2 supra-alar bristles present; thorax strongly depressed. The *stuckenbergi* group shows the following probable autapomorphy: face strongly convex below. Polarity in the characters distinguishing these two groups has been determined by reference to the apparent ground-plan states for the genus *Neurochaeta* (the sister group of *Neurotexis*), and also to some extent by consideration of *Neurocytta* (the out-group next removed), and *Anthoclusia* (the approximate stem-group).

Within the *polyaster* group, monophyly of the clade *N. freidbergi* + *N. polyaster* is supported by the following apomophies: fronto-orbital plates broadened; anterior part of mesopleuron very strongly sloping mesad from upper margin to coxal cavity; abdominal tergites two to six with silvery-pruinescent desclerotised spots. The sister group of the above clade is the species *N. vesca*, with the following notable apomorphies: pigmentation much reduced; costal lappet vestigial.

Within the *stuckenbergi* group cladistic relationships are more difficult to determine. Male postabdominal characters are not among the most suitable characters for this analysis because they are inherently unstable above the species level (McAlpine, 1988b). The most significant remaining character sequences concern bristling and colouration. I identify three probable clades within the *stuckenbergi* group but do not believe I have sufficient evidence to demonstrate an ordered sequence between these.

1. The species *N. charis* alone is taken as the first clade. This has probably the most plesiomorphic development of the dorsocentral bristles as indicated by similarity to the apparent stem group *Anthoclusia*. *Neurotexis charis* is not so close to the other two clades as to suggest that either of the latter is a derivative from within existing populations of this species though individuals show more variation than is apparent for other *Neurotexis* species.

2. *Neurotexis primula* is considered to constitute a clade distinguished inter alia by reduction of dorsocentral bristles to one pair (probable apomorphy) and the robust, deep, dorsally convex thorax (perhaps a plesiomorphy or reversal by comparison with stem group *Anthoclusia*).

3. The species *N. delphis, N. stuckenbergi, N. kaplanae, N. maura, N. despiciens, and N. termon* form a group with the following distinctive apomorphy: mid femur with the proximal bristle of the anteroventral series enlarged. Otherwise these six species have greater development of the costal lappet than any other neurochaetids, a further possible synapomorphy, and agree in having the thorax slightly depressed and the dorsocentral bristles of similar proportions, character states not demonstrably apomorphic though differing from those of the other species of this group. The species *N. delphis* and *N. stuckenbergi* are doubtfully distinct from each other and are therefore provisionally treated as a unit. The remaining *Neurotexis* species *N. kaplanae, N. maura, N. despiciens* and *N. termon* perhaps form a monophyletic group, supported by the following possible synapomorphies as evidenced by outgroup comparison within the *stuckenbergi* group: thorax almost entirely darkly pigmented; surstylus with one or few heavy bristles. The three species *N. maura, N. despiciens* and *N. termon* perhaps form a monophyletic group supported by the following possible synapomorphy as evidenced by comparison with all outgroups in the *stuckenbergi* group: abdominal tergite 2 almost entirely blackish. The apparent sister group of the last three species is *N. kaplanae*, having tergite 2 bicoloured. Host associations are deliberately excluded from the phylogenetic evidence at this stage.

Key to the Species of *Neurotexis*

1. Two supra-alar bristles present; inclinate fronto-orbital bristle inserted anteriorly to foremost reclinate fronto-orbital; lower part of face not or little inflexed, its surface thus not facing ventrally (*polyaster* group) 2

—— One supra-alar bristle present; inclinate fronto-orbital bristle usually not anterior to foremost reclinate one; lower part of face strongly inflexed, thus partly facing ventrally (*stuckenbergi* group) 4

2. General colouration, including bristles, pale yellow; sclerotised fronto-orbital plate narrow, poorly demarcated; costal lappet very short ..... *Neurotexis vesca*

—— General colouration brown-black, with areas of silver-grey to yellow pruinescence and mostly black bristles; sclerotised fronto-orbital plate at least as broad as interfrontal zone, sharply demarcated; costal lappet elongate, defined by a deep incision 3

3. Face convex on lower half in profile; ground colour of interfrontal tawny below greyish pruinescence; pale pruinescence of mesoscutum yellowish, only silvery at sides; major scutellar bristle longer than scutellum ..... *Neurotexis freidbergi*

—— Face straight in profile; ground colour of interfrontal largely dark grey below paler pruinescence; pruinescence of mesoscutum silver-grey; major scutellar bristle shorter than scutellum ..... *Neurotexis polyaster*

4. Mesoscutum yellow, except at anterior extremity; dorsocentral bristles one pair ..... *Neurotexis primula*

—— Mesoscutum predominantly brown to black, with grey pruinescence or yellowish zones; dorsocentral bristles 2 pairs 5

5. Anterior dorsocentral bristle as long as distance between anterior and posterior dorsocentrals; mesoscutum sharply bicoloured, dark brown and yellow; scutellum blackish with pale apex; mid femur with proximal bristle of anteroventral series not enlarged ..... *Neurotexis charis*

—— Anterior dorsocentral bristle much shorter than distance between dorsocentrals; mesoscutum not sharply bicoloured, with fulvous zones, if present, largely obscured by grey pruinescence; scutellum entirely dark; mid femur with proximal bristle of anteroventral series enlarged 6

6. Bristles on antennal segment 2 yellow ..... *Neurotexis stuckenbergi*

—— Bristles on antennal segment 2 predominantly black 7

7. Sternopleuron pale fulvous; mesoscutum brown, usually with posterior fulvous zone more or less concealed by grey pruinescence ..... *Neurotexis delphis*

—— Sternopleuron usually uniformly brown; ground colour of mesoscutum usually entirely brown-black, but surface partly concealed by grey pruinescence 8

8. Terminal segment of mid and hind tarsi brown; male: hind femur with a series of ventral bristles extending well distad of midlength; surstylus swollen near middle of anterior margin, narrowed basally ..... *Neurotexis maura*

—— Terminal segment of mid and hind tarsi yellowish or faintly browned; male: hind femur with a series of ventral bristles confined to basal half or almost so; surstylus not narrowed basally 9

9. Abdominal tergite 2 yellowish on about anterior half, brown posteriorly; male: lateral margin of tergite 6 with at least one other bristle more than half as long as large bristle at posterolateral angle; distiphallus sub-basally on right side with elongate denticles about 4.0 µm long ..... *Neurotexis kaplanae*

—— Abdominal tergite 2 almost entirely dark brown; male: lateral margin of tergite 6 with no other bristle over half as long as major posterior one; sub-basal denticles on distiphallus shorter, conical or vestigal 10

10. Male: surstylus in lateral view not broadened basally, with simple apex, with largest bristle situated near or slightly beyond middle of inner surface and at least one third as long as surstylus ..... *Neurotexis despiciens*

—— Male: surstylus in lateral view broad basally and tapered towards midlength, its apex with concave depression on outer surface, bevelled on inner surface, with 2 bristles less than one quarter as long as surstylus at base of bevelled surface ..... *Neurotexis termon*

Neurotexis maura n.sp.

Fig.2

Material examined. HOLOTYPE male, Madagascar: Andasibe (Perinet), 15-16 May 1987, D.K.M. (AM). PARATYPES, 6 males, same data (AM, USNM). Other material (not types), 3 females, same data (AM, USNM).

Description. *Colouration.* Head and its appendages predominantly yellowish; postfrons and antenna tawny-yellow, the former greyish brown centrally; occiput largely blackish brown; cheek bristles yellowish brown to blackish; other major cephalic bristles dark brown to black. Mesoscutum and scutellum entirely brown-black, the former with grey pruinescence centrally and posteriorly; subscutellum with large silvery-white pruinescent central zone; sternopleuron brown-black except for small yellowish area near sternopleural bristle; humeral callus brown. Legs yellow; hind femur blackish on somewhat more than distal half; terminal segment of mid and hind tarsi brown. Wing membrane tinged with brown in costal region; alula brown. Haltere pale yellowish. Abdominal tergite 1 yellowish, tergites 2-6 almost entirely brown-black; in male sternites 3-5 brown-black, in female these sternites generally paler.

Head higher than long; postfrons almost as long as wide; face broadly convex on lower part; fronto-orbital bristles moderately long and strong, the inclinate one inserted slightly behind level of anterior reclinate one, but also somewhat reclinate; inner vertical bristle scarcely shorter than posterior fronto-orbital; postvertical bristles convergent or parallel; vibrissa succeeded by 4 well developed cheek bristles. Antenna with about 5 dorsal rays on basal swelling of segment 6, in addition to more distal dorsal and ventral rays.

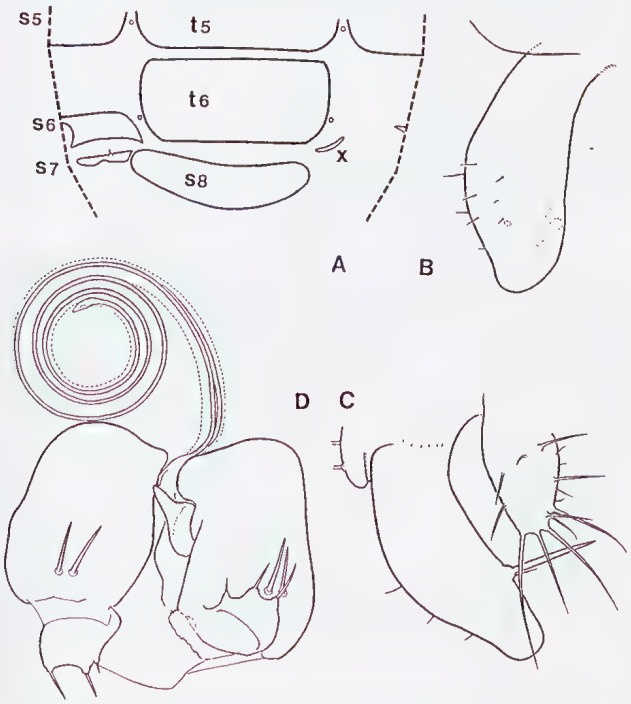

Fig.2. *Neurotexis maura.* A, protandrogram; B, left surstylus, outer aspect; C, left surstylus and cercus, posterior aspect: D, hypandrium and aedeagus. s5-s8 – sternites 5 to 8; t5-t6 – tergites 5 to 6; x – unidentified sclerite.

Thorax rather short, only slightly depressed; dorsocentral bristles 2, anterior one very short and far from posterior one; presutural bristle distinct but small; one supra-alar bristle present; major scutellar bristle much longer than scutellum; one long posterior sternopleural bristle present and sometimes a short one close in front of it. Legs of moderate dimensions; mid coxae well separated; fore femur with 5 or 6 well developed posteroventral bristles, a few weak anterior bristles towards base, and one or few dorsal bristles distally; mid femur with 2-4 anteroventral bristles, basal one much the largest; hind femur in male with a well developed series of ventral bristles which gradually decrease in size beyond middle, in female these bristles replaced by fine hairs; hind tibia with 2 short, thick anteroventral apical spurs, and, in male only, an acute, decurved posteroventral apical tooth. Costal lappet very strong, like that of *N. stuckenbergi*; anal crossvein indistinct; costal index 2.5-2.7; vein 4 index 5.8-7.1.

Abdomen. Male postabdomen: tergite 6 with about 3 lateral bristles of which no other member is more than half as long as posterior member; surstylus elongate, with largely flattened inner surface, with outer surface rather inflated, particularly near middle of length, with base a little narrowed in lateral aspect and overlapped anterolaterally by lobe of epandrium, with apex a little narrowed and compressed, with 2-4 bristles on inner surface beyond middle, of which one or 2 are quite large; each plate of hypandrium with 2 large bristles in front of gonite; gonite short and broad, with 3 bristles on distal margin, the inner one smaller; distiphallus with very few minute denticles on zone beyond base, larger ones about 1.5 µm long.

Dimensions. Total length, male 1.9-2.4 mm, female 2.0-2.4 mm; length of thorax, male 0.8-0.9 mm; female 0.8-0.9 mm; length of wing, male 1.9-2.0 mm, female 1.8-2.1 mm.

Distribution. Madagascar – central eastern district.

Notes. *Neurotexis maura* is among the darkest species of the *stuckenbergi* group, having both the mesoscutum and sternopleuron heavily pigmented. *Neurotexis despiciens, N. kaplanae,* and *N. termon* are similar in this respect, but *N. maura* has the terminal segment of the mid and hind tarsi more strongly browned than is usual in those species. Apart from this slight difference in tarsal colouration, I am only able to distinguish *N. maura* from *N. despiciens* and *N. termon* by male-restricted characters of which the most significant are given in the key to species.

Because *N. maura, N. despiciens,* and *N. termon* were all found on *Pandanus* at Andasibe at the same time, the females cannot be determined by apparent association with males, and no female paratypes are designated.

Etymology. The specific epithet is Latinised from the Greek adjective *mauros*, dark.

Neurotexis despiciens n.sp.

Fig.3

Material examined. HOLOTYPE male, Madagascar: Andasibe (Perinet), 15-16 May 1987, D.K.M. (AM). PARATYPE, 1 male, same data (USNM).

Description. Very similar to *N. maura*, agreeing with description of that species except as indicated below. Female unknown.

Colouration. Terminal segment of mid and hind tarsi indistinctly browned, faintly darker than rest of tarsi.

Thorax. Hind femur with a series of ventral bristles on basal part, rapidly decreasing in length about middle of length of femur and discontinued thereafter; hind tibia as in *N. maura*. Costal index 2.9-3.0; vein 4 index 5.2-5.6.

Abdomen. Male postabdomen: margin of epandrium with less developed lobe than in related species, only slightly overlapping base of surstylus; surstylus moderately elongate, slightly recurved, not incurved, compressed, so as to appear slender and straight in posterior aspect, broadly rounded apically, where it is convex on outer surface, planate on inner surface, near or a little beyond middle of length on posterior part of inner surface with large bristle more than one third as long as surstylus, anterior to this at same level a variable smaller bristle or setula; gonite with 2 bristles; aedeagus with a series of denticles on right side on zone beyond base, larger ones about 2-4 µm long.

Dimensions. Total length about 2.1 mm; length of thorax 0.8-0.9 mm; length of wing 1.8-1.9 mm.

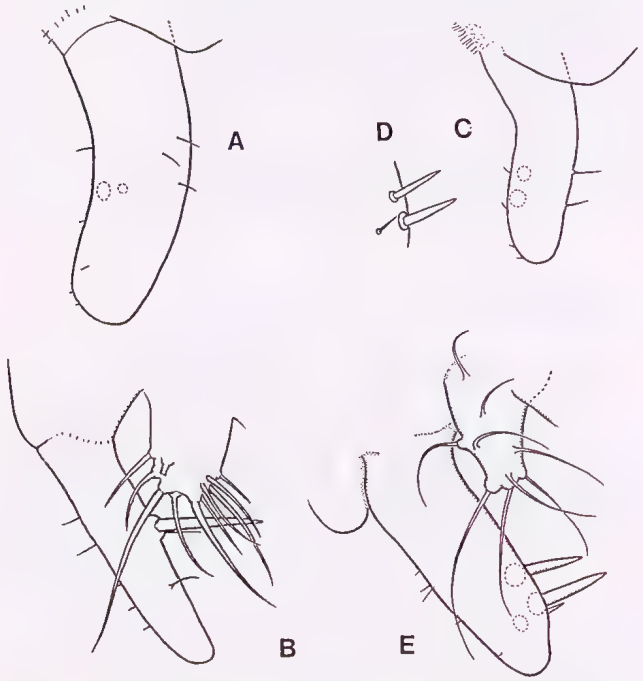

Fig.3. *Neurotexis despiciens*. A, right surstylus, outer aspect; B, left surstylus and cercus, posterior aspect. *Neurotexis kaplanae*. C, right surstylus, outer aspect; D, bristles of last at same scale; E, left surstylus and cercus, posterior oblique aspect.

Distribution. Madagascar – central eastern district.

Notes. *Neurotexis despiciens* is extremely similar to *N. maura, N. termon* and *N. kaplanae*, and is most reliably distinguished by the characters of male postabdomen given in the description and in the key. No females can be referred to the species at present and these should be difficult to distinguish from other species, particularly the sympatric, apparently host-sharing *N. termon*, unless the differences in wing indices prove consistent.

Etymology. The specific epithet is from the Latin participle *despiciens*, looking downwards, in reference to the usual orientation of the insect.

Neurotexis termon n.sp.

Fig.4

Material examined. HOLOTYPE male, Madagascar: Andasibe (Perinet), 15-16 May 1987, D.K.M. (AM). PARATYPES, 21 males same data (AM, BM, PM, TAU, USNM). Other material (not types): 20 females, same data (AM, USNM).

Description. Very similar to *N. maura*, agreeing with description of that species except as indicated below.

Colouration. Terminal segment of mid and hind tarsi slightly browned, most distinctly so on distal part of dorsal surface.

Thorax. Hind femur in male with a series of rather short stout ventral bristles on basal part, which is abruptly discontinued just before middle of length of femur; hind tibia as in *N. maura*. Costal index 2.7-3.2; vein 4 index 6.0-6.8.

Abdomen. Male postabdomen: surstylus in outer aspect slightly broadened basally, tapering thence towards middle, rounded apically, its outer surface at apex slightly concave, inner surface at apex bevelled or chisel-like, two often unequal bristles at base of bevelled surface, ie, much nearer apex than in related species; gonite more narrowed than in *N. maura*, with 2 stout bristles; distiphallus with a series of sharp, conical denticles along right side of sub-basal part, each about 3.0 µm long.

Dimensions. Total length, male 1.7-2.3 mm, female 1.1-2.2 mm; length of thorax, male 0.8-0.9 mm, female 0.8-0.9 mm; length of wing, male 1.8-1.9 mm, female 1.8-2.0 mm.

Distribution. Madagascar – central eastern district.

Notes. *Neurotexis termon* is very close to *N. maura* (q.v. for discussion) and its allies. As in other species

of this complex, the details of the surstylus offer the most decisive specific characters. There is a possibility that the female specimens listed above include some specimens of *N. despiciens*, as I have no information as to how they may be distinguished.

Etymology. The specific epithet is from the Greek noun *termon*, a limit or end, in reference to the terminal modification of the surstylus.

Neurotexis kaplanae n.sp.

Fig.3

Material examined. HOLOTYPE male, Madagascar: Tsimbazaza, Antananarivo (Tananarive), 14 Apr. 1991, A.F. & F.K. (USNM). PARATYPES, 5 males, same data (AM, TAU, USNM); 1 male, Mandraka, 75 km east of Antananarivo, 16 Apr. 1991, A.F. & F.K. (TAU). Other material (not types): 11 females, same data as holotype (AM, TAU, USNM); 1 female, Mandraka, 16 Apr. 1991, A.F. & F.K. (TAU).

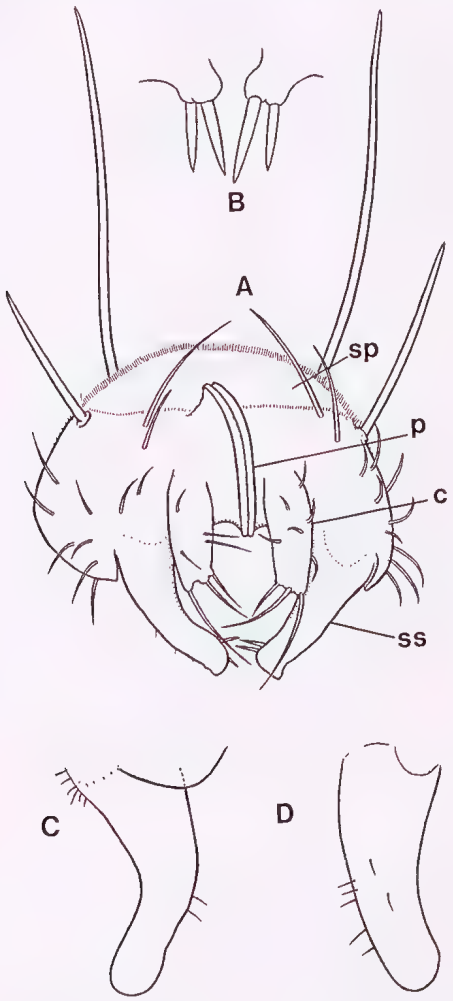

Fig.4. *Neurotexis termon*. A, epandrium and associated structures, posterior aspect; B, gonites, posterior aspect; C, right surstylus, outer aspect. *Neurotexis delphis*. D, left surstylus, outer aspect. c – cercus; p – proctiger; sp – silvery pruinescent zone on epandrium; ss – surstylus.

Description. Very similar to *N. maura*, agreeing with description of that species except as indicated below.

Colouration. Cephalic bristles predominantly dark brown to blackish; cheek bristles usually yellow, sometimes darker. Terminal segment of mid and hind tarsi yellowish, not noticeably darker than preceding segments. Abdominal tergite 2 yellowish on almost anterior half.

Thorax. Hind femur in male with series of ventral bristles occupying short zone before basal third of length of femur. Costal index 2.4-2.9; vein 4 index 5.7-8.0.

Abdomen. Male postabdomen: tergite 6 broad, lateral margin with about 4 bristles, of which at least one other is much more than half as long as posterior one; surstylus moderately elongate, slightly recurved, a little incurved at base only, with apex rounded, convex on outer surface, planate on inner surface, with 2 or 3 thick bristles, often asymmetrically arranged, on distal part of inner surface near posterior side; gonite with 2 large bristles and a small setula; distiphallus with a series of long denticles, each about 4.0 µm long, along right side of sub-basal part.

Dimensions. Total length, male 2.3-2.7 mm, female 2.0-2.5 mm; length of thorax, male 0.7-1.0 mm, female 0.8-1.0 mm; length of wing, male 1.6-2.2 mm, female 1.6-2.0mm.

Distribution. Madagascar – central and central-eastern districts.

Notes. *Neurotexis kaplanae* belongs in the difficult complex of similarly coloured species including *N. maura* (q.v. for discussion). *Neurotexis kaplanae* appears to be generally distinguishable from other species of this complex in the more extensively yellowish anterior zone on abdominal tergite 2, and the paler terminal segment of the mid and hind tarsi. Otherwise determination depends on male postabdominal structures, particularly the stronger bristling of tergite 6, the longer denticles on the distiphallus, and details of the surstylus.

Etymology. The specific epithet refers to the collector, Mrs Fini Kaplan.

Neurotexis delphis n.sp.

Fig.4

Material examined. HOLOTYPE male, Madagascar: Emoty, near Fort Dauphin (Taolanaro), 19 May 1987, D.K.M. (AM). PARATYPES, 9 males, 18 females, same data (AM, BM, NAT, USNM); 6 males, 25 females, south of Mahatalaky, Fort Dauphin district, 18 May 1987, D.K.M. (AM, CNC, MNM); 1 male, 5 km west of Fort Dauphin, 21 Apr. 1991, A.F. & F.K. (TAU); 2 males, 3 females, Fort Dauphin, 18-23 Apr. 1991, A.F. & F.K. (TAU); 1 female, Ranomafana, 800 m, 27 Apr. 1991, A.F. & F.K. (TAU).

Description. Resembling *N. maura*, agreeing with description of that species except as indicated below.

Colouration. Postfrons with bristles brown to blackish; cheek bristles yellow or brownish yellow; major bristles of antennal segment 2 black. Mesoscutum and scutellum black to brown-black with largely dark pruinescence and blackish bristles, ground colour of mesoscutum with pair of yellowish tawny zones posteriorly of very variable extent but each zone usually enclosing both dorsocentral bristles of that side, sometimes zones fused medially; a large zone of pale grey pruinescence covering central and posterior part of mesoscutum, as in *N. maura*, somewhat obscuring yellowish tawny zones; mesopleuron largely dark brown; sternopleuron yellow. Hind femur blackish on slightly less than distal half; terminal segment of mid and hind tarsus variably browned. Wing membrane tinged with brown at apex; alula brown. Abdominal tergite 2 broadly pale yellowish on anterior part; tergites 3 to 6 with variable pale yellowish anterior zones, often absent in male; abdominal sternites predominantly pale yellowish in female, posterior ones variably browned in male. Hind femur of male with about 4 ventral bristles on basal third of its length only; hind tibia of male with well developed almost straight acute apical posteroventral tooth. Costal index 2.6-3.2; vein 4 index 4.8-6.5.

Abdomen. Male postabdomen: surstylus elongate, slightly curved in a posterior direction, slightly broadened basally, tapered for much of length, with rounded apex, with one or few weak bristles on inner surface near apex, much smaller than in *N. termon, N. kaplanae*, and allied species, little larger than sparse setulae elsewhere on surstylus; each hypandrial plate with 2 closely placed unequal bristles, outer one much more slender; gonite broad basally, narrowed distally (in posterior aspect), with 2 thick terminal bristles; aedeagus with a series of sparse, finely pointed sub-basal denticles on right side, each about 2.4 µm long.

Dimensions. Total length, male 2.1-2.5 mm, female 1.8-2.6 mm; length of thorax, male 0.9-1.0 mm, female 0.8-1.1 mm; length of wing, male 1.9-2.1 mm, female 1.6-2.3 mm.

Distribution. Madagascar – southern and south-eastern districts.

Notes. *Neurotexis delphis* is similar to *N. maura* and its allies (*N. despiciens, N. termon*, and *N. kaplanae*) but is paler, particularly in the entirely yellowish sternopleuron and partly pale ground colour of the mesoscutum. The surstylus of *N. delphis*, with one short bristle, has the bristling less developed than in those species.

For discussion of its relationship to *N. stuckenbergi*, see under that species.

Etymology. The specific epithet is the Greek form of the French *dauphin* (dolphin or French crown prince) in reference to the locality Fort Dauphin, in the vicinity of which the species is common.

Neurotexis stuckenbergi (McAlpine) n.comb.

Neurochaeta stuckenbergi McAlpine, 1978: 283-284, figs 5-8, 12.

Material examined. HOLOTYPE female, Madagascar: Fénérive, Dec. 1955, B.R.S. (PM) - re-examined Sept. 1990.

Distribution. Madagascar – central-east.

Notes. The original description covers most significant features of the type specimen. The venation in my figure 8 (McAlpine, 1978) is slightly distorted because of curvature of the wing, the discal crossvein being more than half as long as the distal section of vein 4. Also the head is not as short as in my Figure 6.

Neurotexis stuckenbergi is still only known with certainty from a single female. It seems very close to *N. delphis* and may be conspecific. In view of the often small differences between species, sometimes not apparent in females, the fact that none of the long series of *N. delphis* has pale major bristles on antennal segment 2 as in the type of *N. stuckenbergi*, and the lack of information on the host plant of the latter species, I provisionally regard these as separate species. The type of *N. stuckenbergi* is somewhat faded, but was less so when I drew up my description in 1977. I do not think fading accounts adequately for the difference in bristle colouration.

Neurotexis charis n.sp.

Fig.5

Material examined. HOLOTYPE male, Madagascar: vicinity of Emoty, Fort Dauphin (Taolanaro) district, 19 May 1987, D.K.M. (AM). PARATYPES, 1 male, 2 females, south of Mahatalaky, Fort Dauphin district, 18-19 May 1987, D.K.M. (AM); 1 male, north of Fort Dauphin, 20 May 1987, D.K.M. (AM); 18 males, 32 females, Fort Dauphin, 18-23 Apr. 1991, A.F. & F.K. (AM, BM, TAU, USNM); 9 males, 6 females, 5 km west of Fort Dauphin, 21 Apr. 1991, A.F. & F.K. (TAU, USNM). Other material (not types): 1 female, An'obo, 190 m, Forêt Antsingy, Antsingy, Antsalova district, about 18°45'S 44°50'E, Sept. 1957, P. Griveaud (NAT); 5 males, Tsimbazaza, Antananarivo, 14 Apr. 1991, A.F. & F.K. (AM, TAU, USNM); 1 male, 2 females, Andasibe (Perinet), 16-17 Apr. 1991, A.F. & F.K. (TAU); 3 males, 6 females, Ranomafana, 800 m, 27 Apr. 1991, A.F. & F.K. (AM, TAU).

Description. *Colouration.* Head and its appendages pale yellowish; occiput largely brown; inner and outer vertical, ocellar, fronto-orbital, and postgenal bristles, and dorsal bristles on antennal segment 2 brown to black, other cephalic bristles pale yellowish. Thorax brown-black with black to brown bristles and setulae, those setulae on sternopleuron yellow; mesoscutum with large yellow zone extending from scutellar suture to in front of centre and laterally to postalar bristle; humeral callus tawny; scutellum with yellow apex; subscutellum with

large, shining, silvery-white pruinescent central zone, brown laterally. Legs yellow; distal quarter of hind femur blackish. Wing hyaline, with yellowish veins; alula greyish. Haltere pale yellowish. Abdominal tergites 3-7 and posterior part of tergite 2 brown, remainder of tergites pale yellowish; ventral surface of abdomen pale yellowish, with lateral margins brown, more broadly so posteriorly and more extensively so in male than in female; epandrium with large silvery-white pruinescent zone.

Head higher than long; postfrons, near middle, nearly half as wide as head; face, on lower part, broadly convex, receding toward epistomal margin; fronto-orbital bristles moderately long and strong, the inclinate one inserted slightly behind level of anterior reclinate one, incurved but not at all reclinate; inner vertical bristle shorter than fronto-orbitals; postvertical bristles parallel; vibrissa succeeded by 3 or 4 cheek bristles of similar size. Antenna: segment 6 of arista with dorsal rays 5 or 6 on basal part, 3 distally with gap beyond first, ventral rays 3 or 4, all distal, medial rays 2-4, all distal, and with short terminal fork.

Thorax rather short and robust, dorsally convex; 2 unequal dorsocentral bristles present, posterior one conspicuously longer than scutellum, anterior one at least as long as its distance from posterior one; presutural bristle distinct; prescutellar acrostichal bristle absent; only 1 distinct supra-alar bristle (as distinct from postalar) present; major scutellar bristle much longer than scutellum; a long posterior sternopleural bristle present, with somewhat shorter bristle close in front of it, but sternopleuron without anterior bristles or special group of setulae. Legs of moderate dimensions; mid coxae approximated but not contiguous; femora increasing in length in the order fore, mid, hind; fore femur with 5-7 dorsal bristles, about 5 large posteroventral and no anteroventral bristles; mid femur with a series of up to 7 short anterior to anteroventral bristles; hind femur with a large anterior bristle at about apical fifth, 1 large dorsal bristle at about same level, 1 or 2 smaller dorsal bristles further basad, and some weakly differentiated ventral bristles near base; mid tibia with about 5 short, thick black apical anterior setulae, and a large straight apical ventral spur; hind tibia with 2 small but well differentiated apical anteroventral spurs. Costa produced at subcostal break into an elongate lappet which is shorter than that of *N. stuckenbergi* and *N. polyaster*; anal cell narrow; anal crossvein strongly bent; vein 6 somewhat sclerotised; costal index 2.2-2.4; vein 4 index 4.2-5.3.

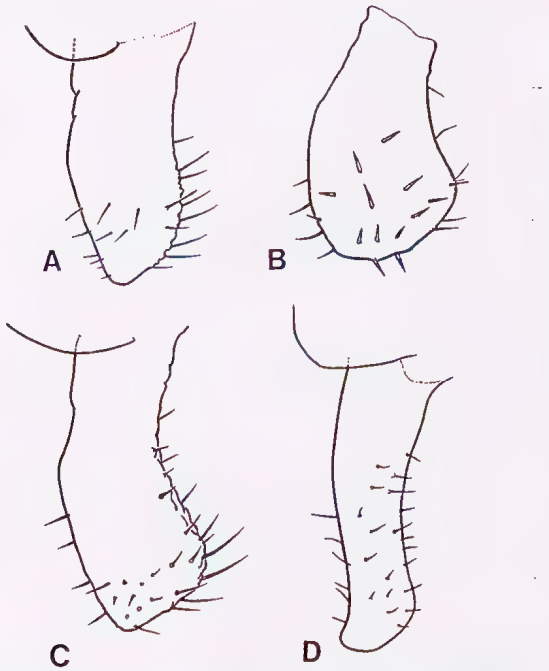

Fig.5. Left surstylus, outer view, of *Neurotexis* spp. A, *N. charis*, holotype; B, *N. charis*, near Mahatalaky, detached; C, *N. charis*, Fort Dauphin; D, *N. primula*.

Abdomen broad. Male postabdomen somewhat similar to that of *N. maura*; surstylus very variable in shape, typically about 2.4 times as long as broad in outer aspect, parallel-sided or variably expanded distally, a little curved in posterior direction, often subangular anteriorly at the slightly outwardly curved apex, sometimes much broadened distally or obovate-spatulate, setulose in part but without strong bristles, its surface with very variable, often reticulate rugosity; each hypandrial plate with 2 long bristles; gonite more elongate than in *N. maura*, with 3 long, more or less unequal bristles.

Dimensions. Total length, male 1.5-2.1 mm, female 1.6-2.4 mm; length of thorax, male 0.6-0.8 mm, female 0.6-0.9 mm; length of wing, male 1.4-1.8 mm, female 1.5-1.9 mm.

Distribution. Madagascar - widely distributed.

Notes. *Neurotexis charis* is apparently a remarkably variable species, though the essential characters given in the key are constant in the available series of 76 examples. Specimens from Ranomafana, Andasibe, and one from Tsimbazaza have the mid femora largely blackish and hind femora more extensively so than in other specimens, but male genitalia characters match those of typical specimens with paler femora. The shape of the surstylus is surprisingly variable, but apparently shows no group consistency which could be used to distinguish closely related species, nor does the variation fit a geographic pattern. This is in sharp contrast to the group of very similar species including *N. maura, N. kaplanae, N. termon* and *N. despiciens*, where differences in the surstylus are evidently specific.

Etymology. The specific epithet is from the Greek *charis*, grace or beauty.

Neurotexis primula n.sp.

Figs 1, 5

Material examined. HOLOTYPE male, Madagascar: Emoty, near Fort Dauphin (Taolanaro), 19 May 1987, D.K.M. (AM).

PARATYPES, 2 males, 8 females, same data (AM); 6 males, 23 females, south of Mahatalaky, Fort Dauphin district, 18 May 1987 (AM, BM, NAT); 8 male, 36 female, Fort Dauphin, 18-23 Apr. 1991, A.F. & F.K. (TAU, USNM); 1 male, 1 female, 5 km west of Fort Dauphin, 21 Apr. 1991, A.F. & F.K. (TAU).

Description. *Colouration.* Head creamy white; postfrons pale yellow; bristles on postfrons yellowish brown, those on cheek yellow, those on antennal segment 2 yellowish brown to dark brown. Antenna pale yellow, Proboscis and palpus deeper yellow, slightly paler ventrally, with dorsal bristles and hairs dark brown, other bristles and hairs paler; mesoscutum with short, broad dark brown zone, largely concealed by head, at anterior extremity; scutellum dark brown with large orange apical zone; subscutellum dark brown laterally, with large, shining silvery-pubescent central zone. Legs yellow, about apical fifth of hind femur brown-black. Wing hyaline, with yellowish veins. Haltere pale yellowish. Abdominal tergite 1 and much of tergite 2 yellow, remainder of tergites yellowish to brown (very variable in the dried material, females often paler); in male, epandrium with large silvery-pubescent zone; ventral surface of abdomen yellowish, with variable brown suffusion.

Head of somewhat similar proportions to that of *N. charis* and *N. stuckenbergi*; fronto-orbital bristles slightly longer than in the above species; inclinate fronto-orbital strongly incurved, not at all reclinate, inserted well behind level of anterior reclinate bristle; postvertical bristles parallel, thicker than in other species. Antenna as described for *N. charis*.

Thorax similar to that of *N. charis*, less depressed than in *N. maura, N. delphis*, and allied species; only the long posterior dorsocentral bristle present; 2 unequal posterior sternopleural bristles present. Legs similar to those of *N. charis*; hind femur with a series of short, strong, dark ventral bristles near and before middle in male, much reduced and pale in female. Costal lappet similar to that of *N. charis*; costal index 2.4-2.8; vein 4 index 3.5-5.3.

Abdomen. Male postabdomen generally as described for *N. delphis*; surstylus elongate, slightly compressed at the rounded apex, not broadened basally, with numerous short setulae; each hypandrial plate with 2 widely spaced bristles, outer one particularly long; gonite somewhat elongate, with 2 apical bristles and a small anterior setula, and a rounded anterior projection at base.

Dimensions. Total length, male 1.9-2.4 mm, female 2.0-2.6 mm; length of thorax, male 0.8-0.9 mm, female 0.9 mm; length of wing, male 1.7-2.0 mm, female 1.8-1.9 mm.

Distribution. Madagascar – south east.

Notes. *Neurotexis primula* differs from other species of the *stuckenbergi* group in having a single pair of dorsocentral bristles and the yellow thorax with very little darker colouration. In the field the yellow colour with conspicuous brown eyes (when viewed with a magnifying loupe) helps identification. *Neurotexis vesca* has somewhat similar colouration, but the thorax is much depressed.

Etymology. The specific epithet is from the Latin noun *primula*, a primrose, in reference to the colouration.

Neurotexis vesca n.sp.

Fig.6

Material examined. HOLOTYPE female (unique), Madagascar: south of Mahatalaky, Fort Dauphin (Taolanaro) district, 18 May 1987, D.K.M. (AM).

Description of female (male unknown). *Colouration.* Yellow dorsally, creamy-white ventrally; bristles and hairs pale yellowish; specialised silvery pruinescence absent from all parts. Antenna, legs, and haltere pale yellowish. Wing clear, with yellow veins; costal bristles and spinules brown.

Head slightly depressed, height about 0.8 of length; width of postfrons near middle 0.53 width of head, its length slightly less than width; fronto-orbital plate most strongly sclerotised along eye margin, not demarcated on medial side from the apparently broad mesofrons, extensively setulose, but with single almost regular series with posteriorly curved apices close to eye margin; fronto-orbital bristles quite short (middle reclinate one differing much in position between right and left sides of holotype); postvertical bristles strongly divergent; cheek bristles as in *N. polyaster*; eye narrowly oblique. Antenna with ventral bristle on segment 2 fine, not reaching beyond centre of face.

Thorax moderately depressed, broadest across the prominent, tumid humeral calli; postnotal structures not as deep as in *N. primula* and related species, less dorsoventrally compressed than in *N. polyaster*; chaetotaxy similar to that of *N. polyaster*; anterior sternopleurals absent. Legs relatively longer than in *N. polyaster*, more slender than in all other *Neurotexis* spp.; fore femur with dorsal bristles less strongly differentiated than in *N. polyaster*, with 3 or 4 posteroventral bristles; mid femur with poorly differentiated anterior bristles; hind femur tapered and slightly curved basally, with one anterior bristle at about apical quarter and 3 dorsal to anterodorsal bristles, one near middle of length and 2 more distally placed; mid tibia with armature slightly weaker than that of *N. charis*; hind tibia with one weakly differentiated apical anteroventral bristle. Costa with very short lappet at subcostal break, surmounted by rather short terminal bristle; anal cell narrow; anal crossvein indistinct; costal index 3.3; vein 4 index 5.5.

Abdomen moderately broad, only sternites 4 and 5 as broad as tergite of respective segments, only sternites 5 and 6 with distinct bristle at each posterolateral angle;

cercus tapering near base, slender for much of length, with several moderately long setulae.

Dimensions. Total length 2.2 mm; length of thorax about 0.9 mm; length of wing 2.0 mm.

Distribution. Madagascar – south-east.

Notes. *Neurotexis vesca* is apparently related to *N. freidbergi* and *N. polyaster* because of the two supra-alar bristles, scarcely convex face, and depressed form. It is distinguished from all other species of *Neurotexis* by the vestigial costal lappet, absence of shining silvery pruinescence on the subscutellum and elsewhere, and entirely pale yellowish thorax.

Etymology. The specific epithet is a Latin adjective, wasted or thin, in reference to the small size and slender body and legs.

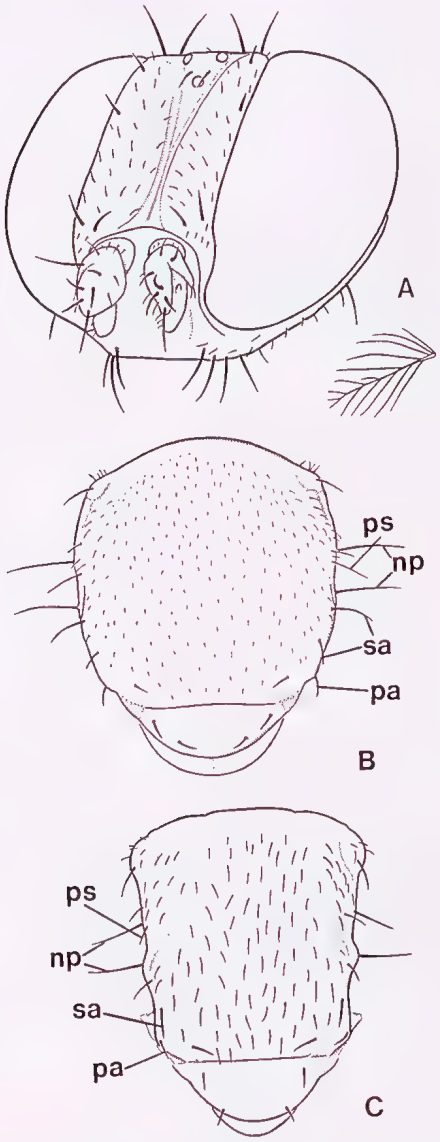

Fig.6. *Neurotexis polyaster.* A, head, left arista (segment 6) shown separately; B, thorax, dorsal aspect. *N. vesca.* C, thorax, dorsal aspect. np – notopleural bristles; pa – postalar bristle; ps – presutural bristle; sa – supra-alar bristles.

Neurotexis freidbergi n.sp.

Fig.8

Material examined. HOLOTYPE male, Madagascar: Fort Dauphin (Taolanaro), 18-23 Apr. 1991, A.F. & F.K. (USNM). PARATYPES, 10 females, same data (TAU, USNM, AM).

Description. Characters as given for *N. polyaster*, except as indicated.

Colouration. Fronto-orbital plate grey-black, with silvery pruinescence; interfrontal tawny, with greyish white pruinescence; face, parafacial, and anterior part of cheek greyish brown; postvertical and all strong cheek bristles black. Antenna yellowish grey, with segment 2 partly darker. Labella tawny to brownish. Mesoscutum with shining pruinescence abruptly bicoloured, largely yellowish with narrow silvery lateral zones demarcated by dorsocentral lines. Hind femur yellowish at base, scarcely yellowish at apex; fore tibia with large blackish brown zone not reaching extremities. Abdominal tergites with desclerotised spots arranged as in *N. polyaster*, but broader and, in female, less brilliantly shining in posterior aspect, in male absent from tergite 6; epandrium of male with silvery pruinescent posterior zone; abdominal sternites yellowish brown to dark brown.

Head not depressed, higher than long; postfrons near middle 0.31-0.32 as wide as head, 1.6-1.7 times as long as wide, markedly narrowing posteriorly; fronto-orbital plate slightly variable, anteriorly usually markedly broader than interfrontal; interfrontal concave anteriorly but without linear groove, broader than in *N. polyaster*; fronto-orbital bristles, particularly the 2 anterior pairs, larger than in *N. polyaster*; inner vertical bristles larger than in *N. polyaster*, more closely placed and usually crossed near apices; usually 5 large and one or 2 smaller cheek bristles behind vibrissa. Antennal segment 2 with one well differentiated but not large ventral bristle; arista with about 9 dorsal rays (not including terminal fork and shorter medial rays).

Thorax of similar form to that of *N. polyaster* but only moderately depressed and slightly less broad; most thoracic bristles longer than in *N. polyaster*; major scutellar bristles longer than scutellum, less widely separated than in other *Neurotexis* species. Fore femur with about 7-11 dorsal to posterodorsal bristles. Wing broader than in other *Neurotexis* species; costal index 2.3-2.6; vein 4 index 5.2-6.9.

Abdomen. In male only sternites 4 and 5, in female sternites 4 to 7 as broad as tergites; male sternite 5 with a series of posterior marginal bristles, least developed medially. Male postabdomen as described for *N. stuckenbergi* except as indicated; surstylus broad, not much tapered, slightly curved, very obtuse. Each paired hypandrial plate with 2 short, stout bristles; gonite somewhat elongate, terminating in 2 divergent spine-like bristles. Spines of basiphallus long and curved. Cercus slightly compressed and subtruncate at ventral end.

Dimensions. Total length, male 4.1 mm, female 3.7-4.1 mm; length of thorax, male 1.4 mm, female 1.4 mm;

length of wing, male 2.9 mm, female 2.6-2.9 mm.

Distribution. Madagascar – south-east.

Notes. *Neurotexis freidbergi*, the largest species of *Neurotexis*, is closely related to *N. polyaster*, but is distinguished by the characters given in the key. It also has more numerous cheek bristles and more dorsal rays on the basal part of antennal segment 6 than in *N. polyaster*.

Etymology. The specific epithet refers to the collector, Dr Amnon Freidberg.

Neurotexis polyaster n.sp.

Figs 6, 7

Material examined. HOLOTYPE female, Madagascar: south of Mahatalaky, Fort Dauphin (Taolanaro) district, 19 May 1987, D.K.M. (AM). PARATYPES, 1 female, Fort Dauphin, 18-23 Apr. 1991, A.F. & F.K. (USNM); 1 female 5 km west of Fort Dauphin, 21 Apr. 1991, A.F. & F.K. (TAU).

Description of female (male unknown). *Colouration.* Fronto-orbital plate brownish densely covered with shining silvery pruinescence; remainder of postfrons dark greyish, dull-pruinescent, interfrontal yellowish at anterior extremity only; face, parafacial, and anterior part of cheek dull yellowish; postgena grey-pruinescent, darker posteriorly, the pruinescence somewhat silvery from certain angles; occiput dull blackish; cephalic bristles, except postvertical and some cheek bristles, black; frontal setulae yellowish. Antenna dull yellowish, with slight brown suffusion; dorsal bristles on segment 2 black. Palpus brown, with pale setulae; proboscis brown with yellowish labella. Thorax with dark brown to blackish ground colour; mesoscutum, except on lateral margin in front of transverse suture, thickly ashy-grey pruinescent, the pruinescence appearing silvery in posterior aspect; pleura largely with dark grey to brown pruinescence; zone on upper part of mesopleuron with lighter grey pruinescence, silvery in posterior aspect; thoracic bristles mostly black. Coxae brown; femora brown-black, narrowly yellowish apically; fore femur yellowish brown ventrally; mid and hind femora yellowish basally; fore tibia tawny-yellow; mid and hind tibiae brown-black, narrowly yellowish basally. Wing clear, with yellowish veins. Haltere tawny, with white capitellum. Abdominal tergites blackish brown; tergite 1 largely brown; tergites 2-6 with transverse, silvery pruinescent, desclerotised spot at each posterolateral angle (spots appearing dull greyish tawny in anterior aspect); epiproct silvery pruinescent; sternites 1 to 6 brown to yellowish brown, usually becoming dark brown laterally.

Head obliquely depressed; postfrons near middle 0.38 as wide as head, about 1.4 times as long as wide; fronto-

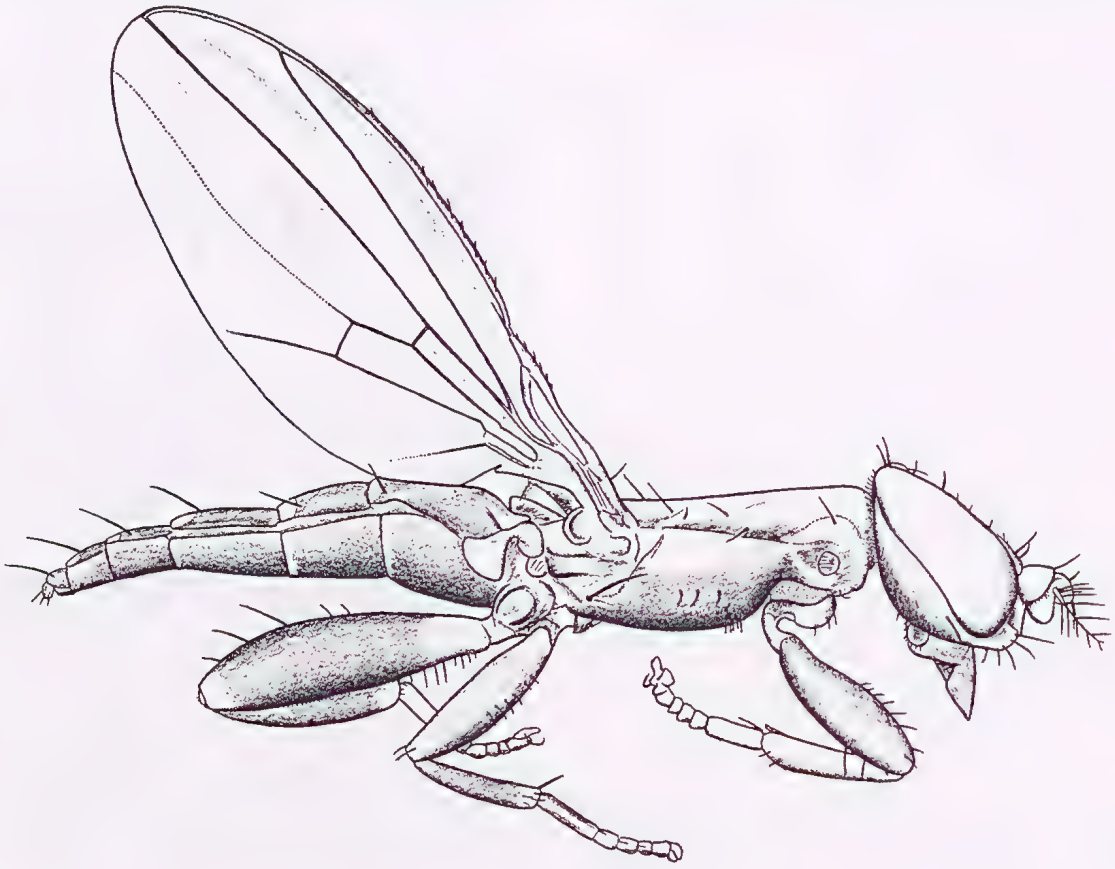

Fig.7. *Neurotexis polyaster* - holotype.

orbital plates very broad, anteriorly very narrowly separated; interfrontal anteriorly with linear median groove; fronto-orbital bristles short but rather stout; postvertical bristles parallel or slightly convergent; 4 cheek bristles behind vibrissa, posterior one or 2 weaker. Antenna similar to that of *N. charis*, but ventral bristle on segment 2 little differentiated from adjacent setulae; arista with 5 or 6 dorsal rays.

Thorax very strongly depressed, broad, but slightly narrowed anteriorly; scutellum and postnotal parts strongly dorsoventrally compressed but structurally similar to those of other *Neurotexis* spp.; chaetotaxy as given for *N. charis* except as follows; dorsocentrals one short pair only; supra-alars 2, posterior one located more dorsally, but not to be interpreted as an intra-alar on account of its longitudinal alignment with postalar; both scutellars shorter than scutellum, major one suberect; posterior sternopleural bristle single, much inclined forwards as in Coelopidae; 3-5 shorter upper anterior sternopleurals, and a tuft of lower anterior sternopleural setulae present; metasternum widely exposed. Legs rather short, hind leg least so; fore coxae not widely separated; mid coxae very widely separated; femora stout, fore and mid ones subequal in length, hind femur longer; fore femur with about 7 dorsal to posterodorsal bristles and 4 or 5 posteroventral bristles; mid femur with about 4 short anteroventral bristles near middle; hind femur with 1 anterior bristle at about apical quarter and a series of about 3 dorsal bristles distally, ventrally near base with fine erect setulae only; mid and hind tibiae as in *N. charis*. Wing as described for *N. charis*; costal index 2.9-3.2; vein 4 index 5.0-6.1.

Abdomen very broad; sternites broad; sternites 4 to 7 as broad as tergites, bristled posterolaterally; cercus short and broad, with one black bristle and minute setulae.

Dimensions. Total length 3.2-3.3 mm; length of thorax 1.2 mm; length of wing 2.3-2.6 mm.

Distribution. Madagascar – south-east.

Notes. *Neurotexis polyaster* is closely related to *N. freidbergi*, but differs in the characters given in the key. The thorax is more strongly depressed than in any other species of *Neurotexis*. In this character it resembles *Neurochaeta magnifica* McAlpine of Papua New Guinea, but, apart from the generic characters, it differs from that species in having the fore coxae relatively close together and the prosternum very narrow.

Etymology. The specific epithet is derived from the Greek *polys*, many, and *aster*, a star, in reference to the shining silvery spots on the abdomen.

Morphology of the Antenna

The antenna of cyclorrhaphous Diptera is primarily a six-segmented appendage, a fact that has often been overlooked. Those asserting the four-segmented nature of the antenna regard the distal part or arista as a single segment, whereas in quite numerous unreduced forms the arista (or stylus) clearly consists of three segments separated by distinct intersegmental membranes. This is quite distinct from the "annulate" condition of the flagellum or parts thereof, in many orthorrhaphous Diptera. As each of the segments generally differs structurally from the others, I prefer to extend the terminology of sequential numbering to cover all six segments, rather than to adopt a special name for each. Segments 4 to 6 are conveniently referred to as the arista, because the articulations between these segments are often difficult to discern in whole dried insects.

With the availability of new material of *Neurocytta* and *Neurotexis*, some aspects of evolution of antennal structure in the Neurochaetidae have become clearer. Groundplan conditions for the family have been determined from the morphology of *Anthoclusia* (so far as it is known in this approximate stem group, Hennig, 1965) and *Neurocytta*, with such periscelidids as *Cyamops* Melander and *Scutops* Coquillett as representatives of a related outgroup (see McAlpine, 1983).

Groundplan characters of the neurochaetid antenna. Segment 2 (pedicel) with distal face hollowed, so that much of distal margin is produced into a lamina; with distal margin deeply slit dorsally, dividing marginal lamina into an inner and outer lobe, these lobes diminishing in width and imperfectly separated ventrally; inner lobe with several thick, spinescent bristles; outer lobe with marginal setulae in a regular, comb-like series; distal margin ventrally without differentiated long bristle. Segment 3 (postpedicel, first flagellomere) ovoid, directed downwards at an angle to longitudinal axis of segments 1 and 2, with thick dorsal basal process fitting into hollow of segment 2; with one sensory pit on outer surface; with group of enlarged microtrichia on apical part. Arista consisting of three sclerotised segments (segments 4-6). Segments 4 and 5 microtrichose, approximately symmetrical, 4 very short, 5 compact but longer than 4. Segment 6 long, consisting of main axis which is slightly symmetrically thickened and irregularly microtrichose basally, distally slender with 2 main series (dorsal and ventral) of hair-like rays.

Neurocytta prisca (Fig.8A) departs from the apparent groundplan in the reduction in number of marginal setulae on the outer lobe of segment 2. It is more primitive than other extant neurochaetids in having segment 2 smaller in relation to segment 3, with less developed lobes and without the long ventral bristle present in *Neurotexis* and *Neurochaeta*, and in the less reduced segment 5. It is uncertain if the shortness of the rays on segment 6 and their absence from its microtrichose basal part constitute a plesiomorphy. What is recorded of antennal structure in the fossil *Anthoclusia* spp. (Hennig, 1965, 1969) is inadequate to resolve the question. If *Neurocytta prisca* is plesiomorphic in this

respect, then there must be convergence in the characters of segment 6 between the *Cyamops* lineage and the more advanced neurochaetids. Convergence here is not improbable in view of some similar features in the arista in such diverse flies as *Nothybus* (Nothybidae) and *Glossina* (Glossinidae).

In *Neurotexis* (Fig.8B,C) segment 2 has enlarged lobes with elaborated armature and a long ventral bristle (probably secondarily reduced in *N. vesca*). Segment 3 has the enlarged apical microtrichia relatively long and, at least in some species (*N. freidbergi* and *N. primula*), minutely branched. Segments 4 and 5 are very small, though freely articulated. Segment 6 has the microtrichose basal part strongly swollen, particularly on the dorsal side (as in *Nothybus*), and has very long dorsal and ventral rays, of which three to six dorsal ones are located on the basal swelling, the first of them at the extreme base of the segment (as in *Cyamops*).

The antenna of *Neurochaeta* has most of these features of *Neurotexis*, except that segment 5 is less reduced, and the branching of the apical microtrichia of segment 3 is apparently absent. Thus antennal morphology supports the idea of monophyly for the group *Neurotexis* plus *Neurochaeta* (Woodley, 1982; McAlpine, 1985a).

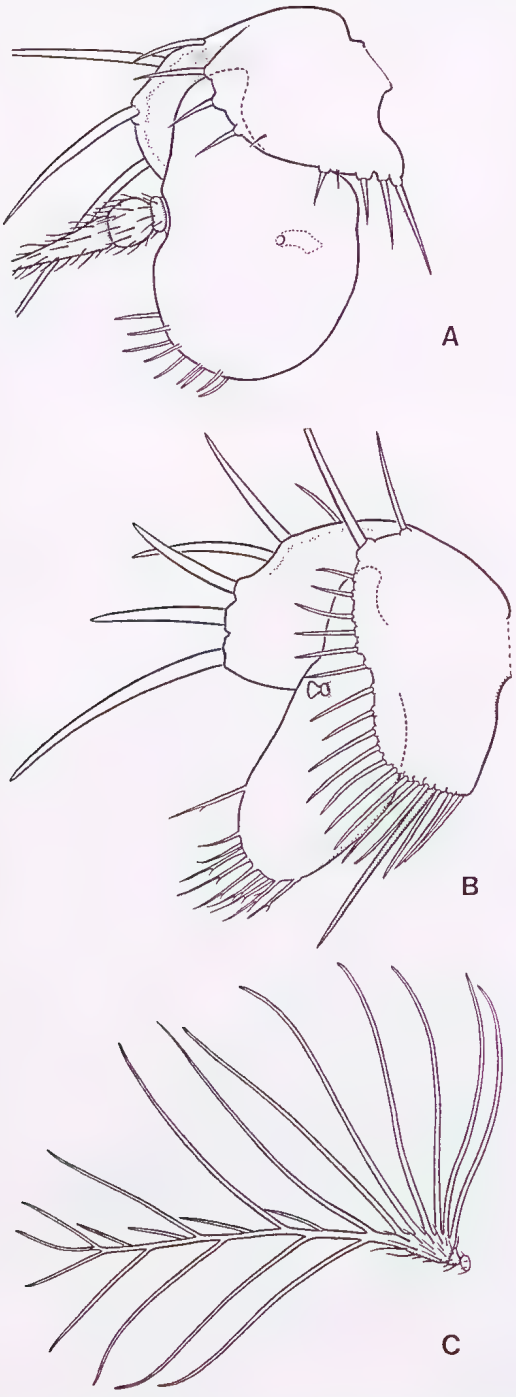

Fig.8. Antennal structures. *Neurocytta prisca*. A, left antenna, segment 1 and part of segment 6 omitted. *Neurotexis freidbergi*. B, left antenna, segments 1 and 6 omitted; C, arista (antennal segments 4-6) at same scale as B.

Field Observations

At 'Banana Grove', Chimanimani National Park, altitude about 1500 m, I found four female adults of *Neurocytta prisca* on suckers (short lateral shoots) less than 1 m high at bases of tall, mature plants of *Strelitzia augusta* Thunberg (family Strelitziaceae, formerly included in Musaceae). These flies could have been fairly numerous in the vicinity, but the leafy crowns of the host plants were out of reach, and access to plants with suckers in the rough terrain was limited by the available time. All plants had single trunks, the suckers apparently not continuing to develop while the main trunk survives. Recruitment rate must be very low, as only three young plants (apparently seedlings) were seen. The plants are of restricted occurrence in the National Park, though numerous at 'Banana Grove'.

The adults of *N. prisca* were seen on leaf blades of *Strelitzia* and one on a petiole, all resting head downwards. They took flight when disturbed.

In a glass tube, adults of *N. prisca* moved less rapidly than the familiar *Neurochaeta inversa*, and not in a zig-zag path. The head downwards position was usually maintained while walking on a vertical surface, but, when at rest, flies did not react promptly to the inversion of the tube (in contrast to spp. of *Neurochaeta* s.str., see McAlpine, 1978). They did not have difficulty in moving from a wall to a ceiling situation, as have *Neurochaeta parviceps* and *N. inversa* (McAlpine, 1988b).

Because two of the specimens obtained on the *Strelitzia* plants were newly emerged (being still teneral more than six hours after capture) it is virtually certain that they were on their host plants.

Numerous adults of *Neurotexis* were found on *Pandanus* (family Pandanaceae, undetermined species) with large, but not broad leaves, growing in damaged forest in a very humid, shaded environment at Andasibe, 15 to 16 May 1987. These flies later proved to be a mixture of *N. termon*, *N. maura* and *N. despiciens*. The flies sheltered within the appressed young leaves in the centre of the plant and ran out when disturbed. They showed similar head-downwards cursorial behaviour to

that of *Neurochaeta inversa* but I judged their movements to be slower. They flew when pressed.

Neurotexis delphis and *N. primula* were found together on *Ravenala madagascariensis* J.F. Gmelin at localities between Fort Dauphin (Taolanaro) and Mahatalaky in south-eastern Madagascar on 18 to 19 May 1987. They were in boggy habitats with *Sphagnum* in otherwise open grassland. The adults of both *Neurotexis* spp. were found in flowers at anthesis. The flowers contained a sugary nectar, attractive to vespids and bees, and also had much powdery pollen. The flies ran or flew out of the flowers when disturbed, often then running on the petioles, particularly on their imbricate bases. Under the rather hot conditions experienced, they were very active, not only running rapidly in the manner of *Neurochaeta inversa*, constantly oriented with the head downwards, but flying readily also, especially individuals of *N. primula*, which showed very frequent aerial escape behaviour. They often settled again within 20 to 40 cm. When observed in a collecting jar, these two *Neurotexis* spp. (and also a single individual of *N. polyaster*) did not run in such definite zig-zag paths as do *Neurochaeta inversa* and *N. parviceps*, but moved more in the manner of inverted *Stenomicra* spp. (see McAlpine, 1978). The single specimen of *Neurotexis vesca* was collected with the above species on flowering *Ravenala* but was not distinguished from the similarly coloured *N. primula* in the field, as it apparently showed similar behaviour.

Neurotexis charis was collected in small numbers together with *N. delphis* and *N. primula* at the above sites on flowering *Ravenala*. On 20 May 1987 I examined a *Ravenala* plant on a hillside a short distance west of Fort Dauphin. When an inflorescence, long past anthesis, was disturbed, several neurochaetids emerged from the bracts. Only one could be captured and proved to be *N. charis*. It exhibited normal (for *Neurotexis*) head-downwards cursorial behaviour.

The numerous specimens of *Neurotexis* obtained by A. Freidberg and F. Kaplan in Madagascar during April 1991 were all taken on *Ravenala madagascariensis* (*in litt.* and label data). These include *Neurotexis kaplanae, N. delphis, N. charis, N. primula, N. freidbergi* and *N. polyaster* (see lists of material examined under these species for localities). They particularly noted the head-downwards cursorial behaviour of these flies.

Discussion of Host Plants

I previously summarised information on neurochaetid host plants in the Australian and Oriental regions (McAlpine, 1988b). These apparent hosts belong in the families Araceae (order Arales), Pandanaceae (order Pandanales), Zingiberaceae and Musaceae (order Zingiberales). The apparent hosts in the Afrotropical Region belong in the families Pandanaceae and Strelitziaceae (order Zingiberales). These latter are inferred to be larval hosts because they are inhabitated by adult flies and offer phytotelmata probably suitable for the larvae. Also, some of the flies were newly eclosed when found, and could not have moved far from their larval habitat.

Because neurochaetids have been rarely sought in the Afrotropical Region, additional host taxa probably remain to be recorded. Likely host genera of Musaceae in the region include *Ensete* and *Musa*, judging from associations with oriental neurochaetids. My colleague D.A. Barraclough has searched for neurochaetids on *Strelitzia* in likely habitats in South Africa (particularly Natal Province), so far without success.

Some recent observations suggest that adult neurochaetids may at times use for shelter plants other than those in which their larvae live. At Palmerston East, Queensland, 25 January 1991, several individuals of *Neurochaeta inversa* McAlpine were seen resting on the large leaves of *Musa* sp. and some were sheltering in the involute young leaves. Other individuals were on their normal host, *Alocasia*, nearby. Hay & Wise (1991) have reidentified Australian mainland populations of *Alocasia* as *A. brisbanensis* (F.M. Bailey) Domin, so this is accepted as the correct name for the host of *Neurochaeta inversa*. This action does not affect the identification for the host of *Neurochaeta macalpinei* Woodley in Sabah and Palawan which is still presumed to be *Alocasia macrorrhizos* (*L*) G. Don. The record of this species from Palawan, Philippines, is due to R. de Keyzer (AM collection).

Apparent hosts are recorded above for all afrotropical neurochaetid species except *Neurotexis stuckenbergi*, but as yet no species has been found on more than one genus of plants. *Ravenala madagascariensis* apparently supports populations of at least seven *Neurotexis* species and five (perhaps 6) species have been found together on the one group of plants near Mahatalaky. The three species I found living together on *Pandanus* at Andasibe are distinct from any found on *Ravenala*. Freidberg and Kaplan collected only on *Ravenala* at this locality and the one specimen of *Neurotexis* they obtained (a female, probably of *N. kaplanae*) is different from any in my much larger sample. These data suggest a high degree of host specificity in *Neurotexis* species.

In Figure 9 I have superimposed the pattern of apparent host plant associations on a phylogeny of neurochaetid species, omitting those relatively few species for which I have no host data.

The phylogeny is that previously worked out (McAlpine, 1988a) expanded to cover additional species. An undescribed species of *Neurochaeta* collected on *Musa* sp. (Zingiberales: Musaceae) in Thailand by R. de Keyzer (AM collection) is referred to as "Thai sp." in Figure 9. As it is extremely similar to *Neurochaeta parviceps* McAlpine and differs mainly in male postabdominal characters, it is placed for present purposes as a sister species of it. A cladistic treatment of the now numerous species of *Neurotexis* is based on the data discussed under that genus. These data leave a few doubtful relationships in the

phylogenetic system. However, for the present purpose of locating changes in host plant taxa, the main relevant points in this clearly monophyletic genus are: (i) the three species forming the *maura* complex (viz. *Neurotexis maura, N. despiciens*, and *N. termon*) are taken as forming a moderately probable monophyletic group, and (ii) it is very improbable that the *maura* complex forms a sister group to a major part of the species of *Neurotexis*. If the *maura* complex is monophyletic, its sister group is probably *N. kaplanae* alone, or perhaps *N. kaplanae* + *N. delphis* + *N. stuckenbergi* (host of the last species unknown).

The pattern of host association shows a predominant preference for plants of the order Zingiberales, which spreads across the three documented fly genera and includes three of the five Old World plant families included in the order (Table 1). Further interesting features of the pattern are: i) *Neurocytta prisca*, which constitutes a relatively plesiomorphic sister group to all or most of the other neurochaetid species, lives on a plant of this order; ii) the species of *Neurotexis*, except for the 3 species of the *maura* complex, probably constituting a monophyletic group of low phylogenetic order, live on plants of this order; iii) three species of *Neurochaeta*, including one which apparently constitutes a relatively plesiomorphic sister group to all other species of the genus, live on plants of this order.

On the basis of the above data, I propose a hypothesis that the plesiotypic host association for extant taxa of Neurochaetidae is that with the Zingiberales, though at present manifested by diverse associations with three known families and four known genera of this order.

The system presented in Figure 9 involves the lowest possible number of host switches, indicated by a circled S, to explain the existing pattern. The association of neurochaetids with the order Pandanales (family Pandanaceae) can be explained by two independent host changes relatively late in neurochaetid history, once in the genus *Neurotexis* in Madagascar, and once in the genus *Neurochaeta* in New Guinea (or a nearby precursory land mass). The association with the order Arales (family Araceae, genus *Alocasia*) is also explicable by two late host changes, each affecting a single known species of *Neurochaeta*, in Australia and Malesia respectively. An equally parsimonious number of host switches in the branch leading to *Neurochaeta inversa* and *N. magnifica* can be obtained by an initial switch, before the furcation of this branch, from Zingiberales to Arales, followed by a switch of one sister species to Pandanales, or vice versa. My only reasons for preferring the system shown in Figure 9 are the weakness of the shared synapomorphies of *N. inversa* and *N. magnifica* and the great degree of morphological divergence between them.

Alternatively, the most parsimonious explanation for the pattern of present host associations may not be the

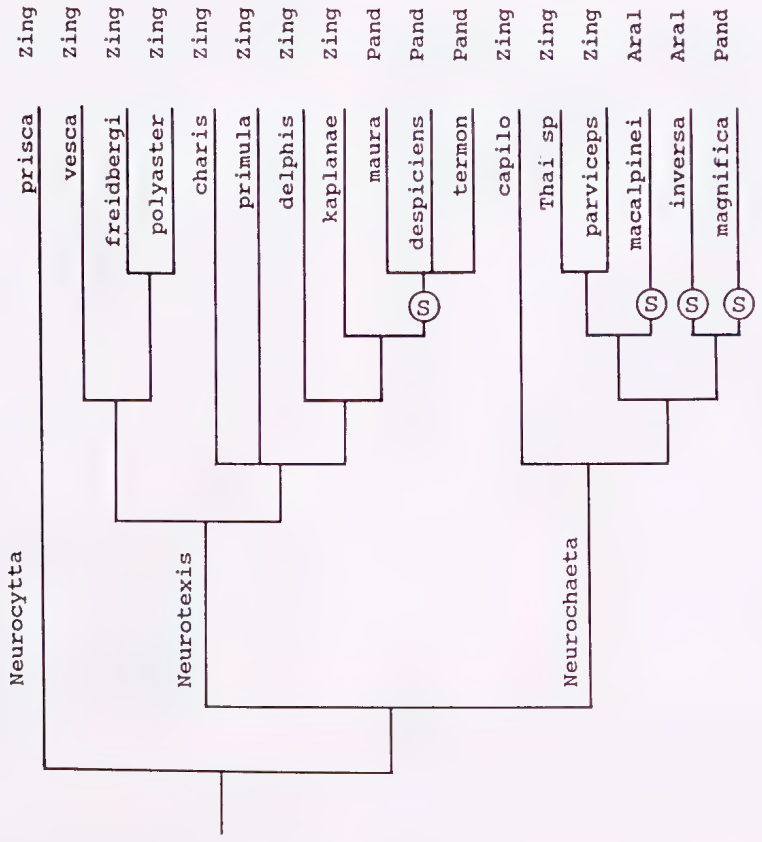

Fig.9. Cladogram of species of Neurochaetidae, showing orders of host plants, fly species with unknown hosts omitted. S – possible points of switch of host order from hypothetical plesiotypic zingiberalean association. Aral – Arales; Pand – Pandanales; Zing – Zingiberales.

historically correct one. There is a possibility of any lineage surviving a temporary loss of access to a zingiberalean host, if it has an accessible alternative host. In view of direct evidence of a number of host switches, the suitability of a number of both zingiberalean and other monocot taxa as neurochaetid hosts, and the long, largely undocumented neurochaetid evolutionary paths, such a host sequence as Zingiberales sp. a —> other monocot sp. —> Zingiberales sp. b is not highly improbable.

The group of zingiberalean families, including Musaceae, Strelitziaceae and Heliconiaceae, was considered as a single family, Musaceae s.l., in older literature (eg, Willis, 1951), and the first two of its components provide host plants for more than half the host-known species of Neurochaetidae. A representative of this plant group is utilised by *Neurocytta prisca*, the recent species which is closest morphologically to the Eocene-Oligocene *Anthoclusia* of northern Europe. The genus *Musophyllum*, which occurred in the arctic in the late Paleocene to early Eocene (Boyd, 1990), is apparently referable to Musaceae s.l., and in the early Tertiary the Nearctic and Palearctic biotas were not very distinct. It is inferred that such zingiberalean plants or related forms may well have been accessible to *Anthoclusia* and may conceivably have been utilised as hosts.

Table 1. Monocot host taxa and associated neurochaetid species.

Zingiberales – Strelitziaceae
- *Strelitzia augusta*
  - *Neurocytta prisca*
- *Ravenala madagascariensis*
  - *Neurotexis vesca*
  - *Neurotexis freidbergi*
  - *Neurotexis polyaster*
  - *Neurotexis charis*
  - *Neurotexis primula*
  - *Neurotexis delphis*
  - *Neurotexis kaplanae*

Zingiberales – Musaceae
- *Musa* spp.
  - *Neurochaeta capilo*
  - *Neurochaeta* sp. (Thailand)

Zingiberales – Zingiberaceae
- *Zingiber spectabile*
  - *Neurochaeta parviceps*

Pandanales – Pandanaceae
- *Pandanus* spp.
  - *Neurotexis maura*
  - *Neurotexis despiciens*
  - *Neurotexis termon*
  - *Neurochaeta magnifica*

Arales – Araceae
- *Alocasia brisbanensis*
  - *Neurochaeta inversa*
- *Alocasia macrorrhizos*
  - *Neurochaeta macalpinei*

Thus, the association between neurochaetids and banana-like plants may have continued for about 40 million years.

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Systematics of the *Perinereis nuntia* Complex (Polychaeta: Nereididae) in South-eastern Australia

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ABSTRACT. Biochemical and morphological analyses show that two species in the *Perinereis nuntia* group occur in south-eastern Australia. The two species are distinguished by fixed differences at 4 of 8 enzyme loci, by non-overlapping ranges of paragnath counts and by qualitative differences in the types of paragnaths present. Previously, all material from south-eastern Australia had been referred to a single species, *Perinereis nuntia*, with two nominal varieties: *P. nuntia vallata* and *P. nuntia brevicirris*. Analysis of intraspecific variation shows that these varieties have no taxonomic significance. Differences between populations, especially those from markedly different sediments, exaggerate intraspecific variation in paragnath counts. Size related variation of paragnath counts is relatively unimportant.

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Sixteen nereidid genera and about 350 species carry chitinous denticles, "paragnaths", on the eversible proboscis (Fauchald, 1977); this amounts to about 40% of all genera and 80% of all species in the family. In most genera paragnaths are arranged in a regular grouping (Fig.1a,b), and counts of paragnaths in each numbered group are the most important character system used by taxonomists to describe and distinguish taxa. Although this system of meristic characters is ideally suited to statistical analysis of intraspecific and interspecific variation, there has been little work of this nature that could guide taxonomic decision-making. Barnes & Head (1977) and Barnes (1978) provided detailed statistical analysis of the ecological significance of variation in paragnath number in several populations of *Nereis diversicolor* Müller, 1776 (also referred to in the literature as *Hediste diversicolor*) but they studied only that species and did not attempt a taxonomic analysis. No taxonomic studies of nereidids have used statistical methods.

Perinereis nuntia and related species comprise a group characterised by an arc of short bar-shaped paragnaths on group VI of the proboscis (Fig.1a). At least 18 nominal species and varieties have been described, of which *P. nuntia* is by far the most widely reported, being recorded from all continents except Antarctica, North America and northern Europe (Wilson & Glasby, 1993). Published descriptions indicate considerable variation in morphology within and between populations, and trinomens have been widely used to identify supposed morphs and geographical races (Fauvel, 1932; Hartman, 1954; Knox, 1960a; Imajima, 1972). Among recent authors, only Paik (1975) and Hutchings & Turvey (1982) have attempted a more critical appraisal of

morphological variability. Paik examined numerous specimens from two localities in South Korea but provided incomplete data and limited analysis; Hutchings & Turvey compared Australian material with specimens from India, China and New Caledonia. Neither of these papers used statistical methods to compare populations and both papers failed to detect consistent differences within *P. nuntia* and recognised only a single species.

My aim in this study was to use electrophoretic analysis of enzymes to establish species boundaries independently of paragnath morphology. Statistical analysis of paragnath counts would then provide a better understanding of intraspecific and (if more than one species was shown to be present) interspecific variation. These results are applied to a worldwide revision of the *Perinereis nuntia* species group by Wilson & Glasby (1993).

All tables are listed in the Appendix.

Biochemical Systematics

Electrophoresis of enzymes is a powerful means of identifying species and is independent of the morphological characters used in traditional taxonomic analysis (Avise, 1975; Ferguson, 1980). Measures of genetic distance such as Nei's Distance (Nei, 1972) are sometimes used in taxonomic studies, but I have followed Richardson *et al.* (1986) in using the proportion of fixed allelic differences as a more practical and biologically sensible indication of species-level differences. (Richardson *et al.*, 1986 showed that, except in extremely polymorphic organisms, the proportion of fixed differences is the major component in calculation of genetic similarity measures.)

Several studies have applied electrophoretic methods to resolve taxonomic problems in polychaetes. A summary of the more rigorous studies illustrates the application of Richardson *et al.*'s fixed allelic difference criterion. Grassle & Grassle (1974, 1976) revealed a complex of 6 sympatric sibling species where a single species, *Capitella capitata*, (Capitellidae) had previously been recognised. Eight enzyme loci were studied and fixed differences were found for virtually all loci between all possible species pairs. Nicklas & Hoffman (1979) found fixed differences at 4 of 7 loci in two morphologically distinct sympatric species of *Glycera* (Glyceridae). Britton-Davidian & Amoureux (1982) found fixed differences at 4 of 9 loci studied and demonstrated that two forms of *Ophelia* (Opheliidae) represent distinct species; morphologically intermediate worms were shown not to be hybrids (as had previously been suggested), but clearly belonged to one or other of the two species. Ekaratne *et al.* (1982) and Crisp & Ekaratne (1984) confirmed the presence of two sympatric sibling species of *Pomatoceros* (Serpulidae); fixed differences were found at 6 of 19 loci studied. The high level of genetic divergence between species in a wide range of families, most usefully shown by the presence of fixed differences at a large proportion of enzyme loci, is clearly a diagnostic criterion in polychaetes as it is in most other animal groups.

Methods

Collection and treatment of samples. Seven sampling localities were chosen in south-eastern Australia to encompass a wide range of habitats. Worms were collected by turning rocks and shallow digging. Such opportunistic collecting probably results in a bias towards larger size ranges, however more objective methods such as sieving sediment fragment many worms. Sample sites are given in the following list (numbers refer to localities shown in Fig.2). Collection dates are followed by a number in parentheses indicating the number of worms collected; samples used for electrophoresis were collected on dates marked with an asterisk.

1. Apollo Bay breakwater, Vic., 38°45'S 143°41'E. Lee shore of artificial breakwater; sediment highly heterogeneous with much quarried rock and some sand

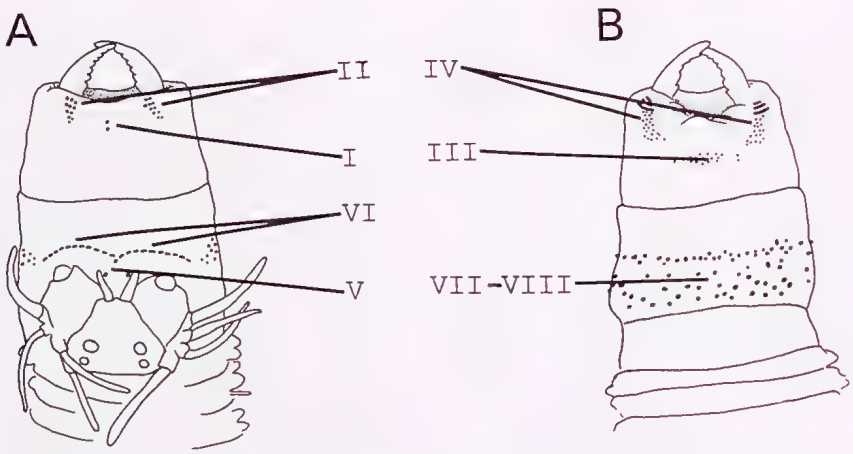

Fig.1. Arrangement of paragnaths in the *Perinereis nuntia* complex (A, dorsal view of extended proboscis; B, ventral view).

and mud fractions present; probably little fluctuation in salinity throughout the year. Dates: 2 Nov. 1984 (20); 30 Oct. 1985 (20); 23 Aug. 1986* (20); 30 Aug. 1987 (20).

2. Mouth of Separation Creek, Vic., 38°38'S 143°54'E. Boulder bed of exposed ocean beach; sediment well-sorted sand; high autumn rainfall and flow from the creek result in seasonal fluctuations in salinity, especially at low tides. Dates: 15 Nov. 1984 (11); 28 Oct. 1985 (20); 13 Apr. 1986* (20); 24 Aug. 1986 (20).

3. Werribee, Melbourne Water main drain, Vic., 37°58'S 144°54'E. Exposed locality in Port Phillip Bay; poorly sorted calcareous sediment with some rocks surrounding mouth of sewage effluent drain; considerable fluctuation in flow results in seasonal variations in salinity and organic input (the locality was described in more detail by Poore & Kudenov, 1978). Dates: May 1985* (21); 18 Sept. 1985 (19); 20 Mar. 1986 (14); 2 June 1986* (20).

4. Flinders, south end of Kennon Cove, Vic., 38°29'S 145°01'E. Sheltered locality in Western Port; poorly sorted muddy sand with seagrass *Heterozostera tasmanica* and some rocks; some fluctuation in salinity due to a small freshwater spring. Dates: 3 Sept. 1984 (21); 7 Oct. 1985 (20); 23 Mar. 1986* (20); 11 June 1986* (20).

5. Quarantine Bay, NSW, 37°05'S 149°54'E. Exposed rocky ocean shoreline with some heterogeneous sediment under rocks; probably little seasonal fluctuation in salinity. Date: 17 July 1987* (2).

6. Batemans Bay, north shore of Clyde River under Princess Highway bridge, NSW, 35°43'S 150°11'E, 17 July 1987. Poorly sorted muddy sand with little rock; salinity probably nearly fully marine with some seasonal fluctuation. Date: 17 July 1987* (7).

7. Coal and Candle Creek, Hawkesbury River estuary, near Akuna Bay, NSW, 33°37'S 151°14'E. Sheltered locality; poorly sorted muddy sand with much rock; salinity probably nearly fully marine but fluctuates due to high rainfall at irregular intervals. Date: 19 Oct. 1986* (5).

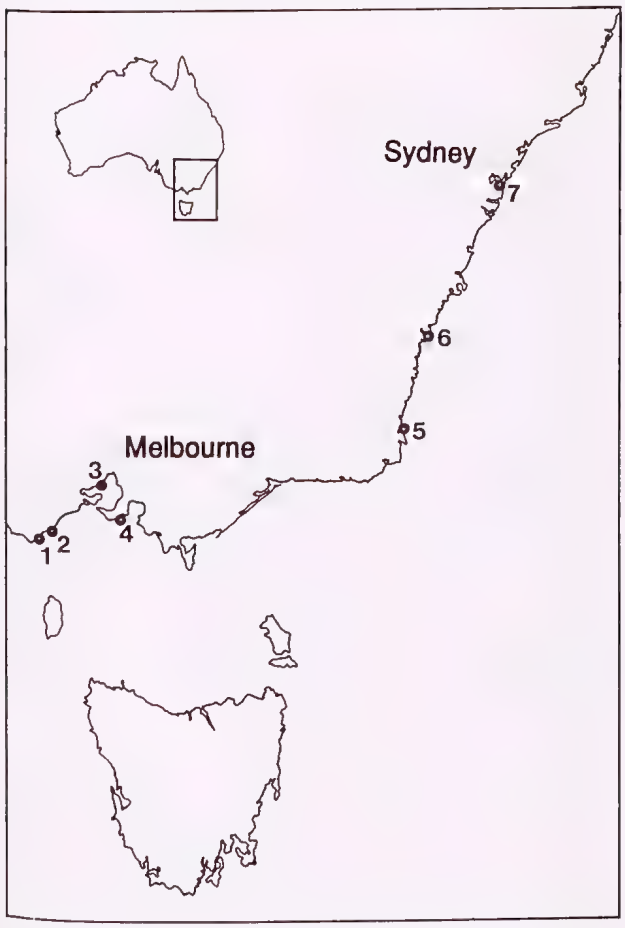

Fig.2. Sample sites referred to in the text.

Sampling strategy and numbers of specimens. Richardson *et al.* (1986) demonstrated that sample sizes of three to five specimens per population are sufficient to allow detection of different species in biochemical systematics. In this study, ten specimens were collected from each of populations 1 to 4, two specimens from population 5, seven from population 6, and four from population 7. Morphological analysis was based on four replicate collections over two years of about 20 specimens from each of sites 1 to 4 (see above). Approximately 80 worms per site were thus analysed; this is of the same order as the sample sizes used by Barnes & Head (1977).

Electrophoretic methods. Worms were kept alive in clean sediment or algae and seawater until returned to the laboratory. In the laboratory individual worms were kept in separate jars of seawater at 16°C for one to four weeks before being used for electrophoresis. Within this period few worms died. A tissue sample comprising two to ten posterior segments was severed from a live worm. The worm was returned to seawater in an individually labelled jar and kept alive to provide further fresh tissue samples. At the conclusion of electrophoretic procedures the remainder of the worm (including the taxonomically crucial proboscis) was preserved in formalin for morphological analysis. The tissue sample was homogenised and run immediately with two to three times its own volume of 0.2 mM Cleland's reagent in distilled water and centrifuged. Electrophoresis was carried out at 4°C using supernatant solutions applied to cellulose acetate supporting gels (Cellogel, Chematron, Milan). Details of buffers, running conditions and stain formulations are provided in Table 1.

Morphological methods. Worms used only for morphological analysis were carried back alive to the laboratory where they were briefly dipped in 95% ethanol. This causes worms to die instantaneously with the proboscis everted (the same method was used by Barnes & Head, 1977), after which they were fixed in 4% formalin and later transferred to 70% ethanol.

A size measure of each worm was obtained by dissecting the proboscis at the base of the right jaw (or the left jaw if the right was damaged) to reveal the full length of the jaw which was measured to the nearest

0.5 mm with an eyepiece micrometer on a stereo microscope. Body size and jaw length in nereidids are linearly related (Olive, 1980; Glasby, 1986) and jaw length measurements have the advantages of being unaffected by preservation technique and can be recorded from broken specimens. Paragnaths in each of the standard "groups" of the proboscis were counted, with left and right side counts distinguished for symmetrical groups. Several distinctive bar-shaped paragnaths were present on group IV in addition to conical paragnaths (Fig.1b); these were recorded separately.

Results

1. Allelic variation. The electrophoretic data (Table 2) were collected to test the null hypothesis "that all 7 populations represent a single species". Two loci, AK and LDH, were monomorphic in all populations. Four loci (AAT, GPI, IDH and MDH) showed fixed differences for alternative alleles at each locus, thus distinguishing populations 6 and 7 from populations 1 to 5. Two further enzyme systems, HK and PGM, stained for multiple bands and showed uninterpretable variation, probably the result of genetic polymorphisms. For both HK and PGM there was evidence of unique alleles in populations 6 and 7, but in the absence of genetic interpretations these data were not utilised further. In terms of genetic distance measures these data are equivalent to Nei's D of 0.69 between populations 1 to 5 and 6 and 7. By the standards of Richardson *et al.* (1986), Nei's D of 0.69 and the existence of fixed differences at 50% of loci is overwhelming evidence for the rejection of the null hypothesis. Two species are present, one represented by populations 6 and 7, the other by populations 1 to 5.

Identification of the two species depends on examination of type material of *Perinereis nuntia* and related taxa. Meaningful reassessment of the type material in turn depends on a better understanding of the nature and significance of inter- and intraspecific variation, which is the goal of this paper. Thus, for the remainder of this paper the northern species (from localities 6 and 7) will be referred to as *Perinereis* sp. A and the southern species (from localities 1-5) as *Perinereis* sp. B. Formal description of these species, with a revision of the *Perinereis nuntia* species-group, is reported separately (Wilson & Glasby, 1993).

2. Intraspecific morphological variability in *Perinereis* sp. B. Three factors which potentially contribute to intraspecific morphological variation in *Perinereis* sp. B were investigated, using paragnath counts and jaw length measurements: size-dependent variation, differences between populations and differences between subspecific morphs. Paragnath data from *Perinereis* sp. B were also used to investigate two additional questions of taxonomic interest: i) are paragnath counts from different groups on the proboscis correlated; ii) are some paragnath counts more variable than others. Sample sizes for *Perinereis* sp. A were too small to analyse intraspecific variation in this species.

Only 16 of 65 possible correlations between paragnath number and jaw length are significant at the 0.01 level and even the highest values generated coefficients of determination (r) values of about 0.2 (Table 3). That is, only about 20% (at most) of the variation in paragnath number can be accounted for by variation in size. A scatter plot of total paragnath number versus jaw length indicates the weak relationship between these quantities and the large amount of variation that is independent of size (Fig.3). Since paragnath numbers in all but group VI are free to increase in two dimensions with growth of the worm, a significant correlation might be expected between paragnath number and the square of jaw length. However, there was no such correlation. There seems to be no simple relationship between size and paragnath number in *Perinereis* sp B.

Numbers of paragnaths in each group are significantly different in about half of all 84 possible pairwise comparisons between population samples (Table 4). The most similar pairs of population samples (in terms of mean paragnath counts) are Apollo Bay and Separation Creek (column A, Table 4), and Werribee and Flinders (column F, Table 4). Canonical variates analysis of the same data (Fig.5) shows some separation of the sampled populations of *Perinereis* sp. B on the first two discriminant functions but does not produce discrete clusters as seen in the interspecific comparison in Figure 4.

Two methods of multivariate analysis were used to look for possible morphs or varieties in *Perinereis* sp. B. Canonical variates analysis was used to determine if differences existed between *a priori* designated groups, and principal components analysis was used as an exploratory technique for investigating intra-specific variation where there is no *a priori* basis for designating groups. Paragnath counts for group V on the proboscis have previously been used as the basis for recognising subspecific varieties of *P. nuntia*. The validity of the named varieties was investigated by assigning specimens from populations 1 to 4 to groups on the basis of 1, 2 or 3 paragnaths present in group V, and canonical variates analysis was performed using the remaining paragnath group counts. This procedure was followed both for the pooled data from populations 1 to 4 and for each population separately. These analyses failed to produce any separation of the designated groups. In all analyses, all specimens plotted in a single cluster and no separation can be seen between the notional subspecific varieties. Principal components analysis of paragnath data also failed to produce any clusters or partial separation of specimens.

The idea that paragnath counts for the different groups on the proboscis might be strongly correlated is relevant because, if so, exhaustive paragnath counts would include some redundant data. Pearson correlation coefficients were calculated between all paragnath groups for all four populations of *Perinereis* sp. B. Coefficients of determination (r) values calculated from these are

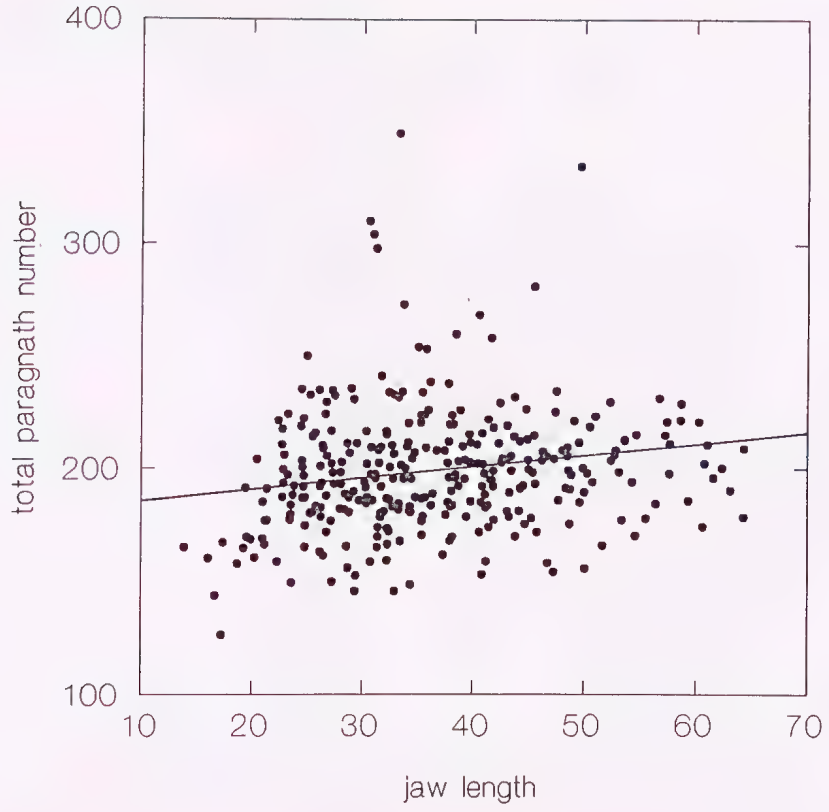

Fig.3. Scatter plot of total paragnath number versus jaw length, *Perinereis* sp. B.

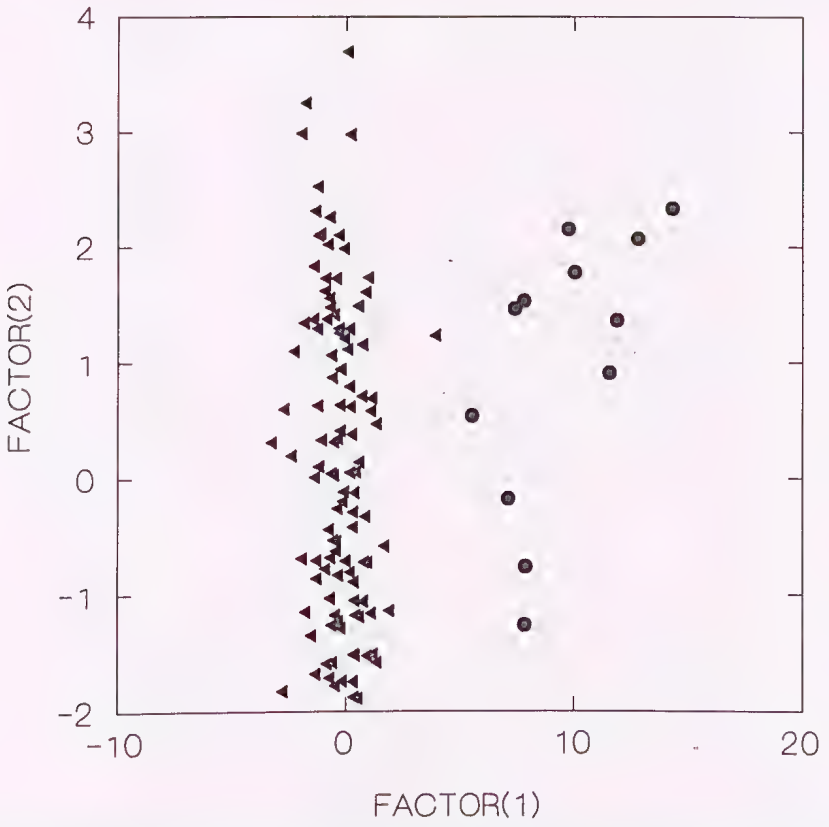

Fig.4. Canonical variates analysis of *Perinereis* spp. A and B based on paragnath counts for groups I, IIL, IIR, III, IVLC, IVLB, IVRC, IVRB, V, VIL, VIR, VII-VIII (circles = sp. A, triangles = sp. B).

low; even for paired symmetrical groups (II, IV, and VI), for which correlation coefficients are significant at p less than 0.01, coefficients of determination are in the range 0.11 to 0.58. That is, only 11% to 58% of the variability in one paragnath group can be accounted for by the opposite pair.

The possibility that there are differences in variability between different paragnath groups is of interest both in terms of taxonomic utility (characters showing little variability are likely to be more useful in taxonomy) and for more fundamental biological reasons (differences in variability between characters might reflect different selective pressures operating or differences in genetic control of expression of the characters). Relative variability of characters is measured by the coefficient of variation (Sokal & Rohlf, 1981); these data are provided for *Perinereis* sp. B in Table 5. Sokal & Brauman (1980) provide a test for comparing coefficients of variation of two dependent (correlated) variables based on the t-distribution. By this method there are no significant differences in the variability of paragnath groups II, III, IV (cones) and VII-VIII within any of the study populations. (Paragnath groups I, IV (bars), V and VI differ in their probabilities of a zero measurement or have different dimensions. Lande (1977) showed that it is not valid to compare coefficients of variation of such characters and these were therefore excluded from inter-character comparisons.) Another possibility is that differences in the variability of the same character might be evident between different populations, but by Sokal & Brauman's (1980) test there are no significant differences in variability of paragnath counts between any of the 4 Victorian populations of *Perinereis* sp. B.

3. Interspecific differences between *Perinereis* spp. A and B. The paragnath data show both quantitative and qualitative differences between the two species. Canonical variates analysis of the same data (Fig.4) differentiate the two species clearly: *Perinereis* sp. A is represented by a cluster distinct from *Perinereis* sp. B. In contrast, although there is some separation of populations 1 to 4 of *Perinereis* sp. B on the first two discriminant functions, there are no discrete clusters. (The two specimens representing population 5 of *Perinereis* sp. B, are morphologically and geographically intermediate between the other populations of *Perinereis* spp. A and B, however the electrophoretic data unequivocally identify these specimens as *Perinereis* sp. B.) Canonical loadings from the canonical variates analysis highlight those dependent canonical factors (paragnath groups) which best separate the populations (Table 6). Oral ring paragnath counts (groups V, VI and VII-VIII) contribute most to factor 1, which separates the two species. In contrast, maxillary ring paragnath counts (groups I, II, III and IV) load more highly on factor 2. Some separation of populations within species occurred along factor 2, although this information could not legibly be presented in Figure 4, which shows the interspecific comparison. Frequency histograms of those

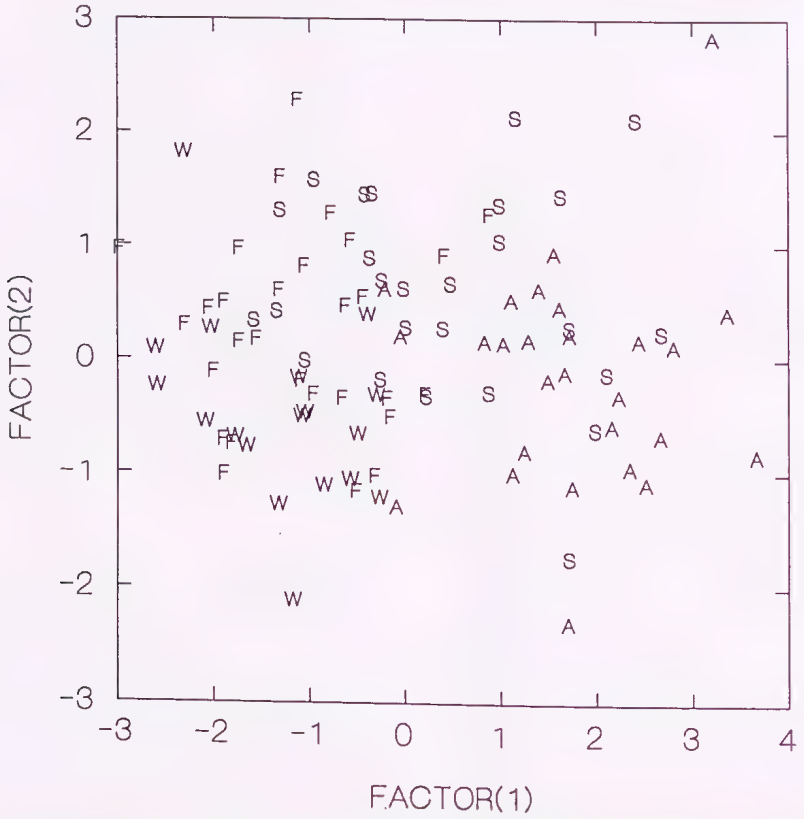

Fig.5. Canonical variates analysis of samples from four localities for *Perinereis* sp. B based on paragnath counts for groups I, IIL, IIR, III, IVLC, IVLB, IVRC, IVRB, V, VIL, VIR, VII-VIII (A = Apollo Bay, S = Separation Creek, W = Werribee, F = Flinders).

paragnath groups identified by the canonical variates analysis, Areas II, VI and VII-VIII, show little overlap between the two species (Fig.6). No intraspecific comparisons of populations show differences of this order.

Finally, re-examination of the specimens revealed a qualitative difference that distinguishes the two species. *Perinereis* sp. A specimens carry an additional band of minute conical paragnaths ventrally on Area VII-VIII. This band is posterior to, and in addition to,

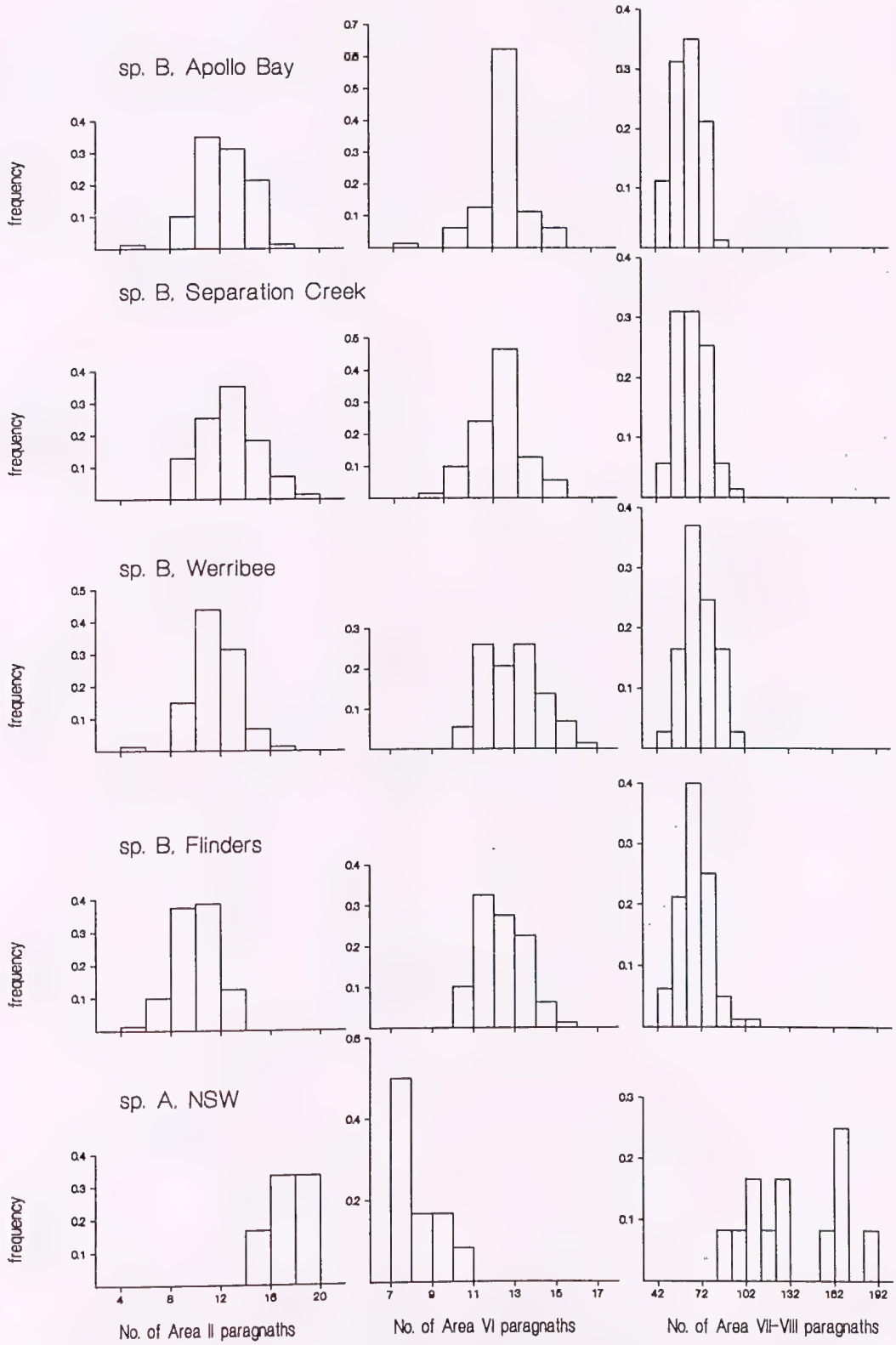

Fig.6. Frequency histograms of paragnath counts for selected groups, *Perinereis* spp. A and B.

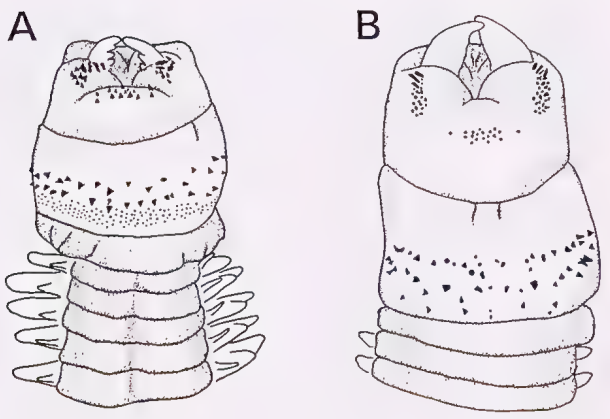

Fig.7. Ventral view of extended proboscis, *Perinereis* spp. A and B.

the irregular double row of larger conical paragnaths that is present in both species (Fig.7).

Discussion

Previous treatments of *Perinereis nuntia* and related taxa suffer from the basic handicap that the level of intraspecific morphological variability was unknown, as was the true taxonomic significance of supposedly diagnostic characters. In this study I have relied on genetic differences between species (as determined by electrophoresis of enzymes) to establish species boundaries independently. Analysis of variation in paragnaths from the same populations shows that differences between populations contribute more to intraspecific variation than differences due to size. Canonical variates analysis of paragnath data separates species convincingly and efficiently, and allows the characters that account for most of the separation of species to be quickly identified. The two species studied can be distinguished on the basis of having non-overlapping ranges of paragnath counts and from qualitative differences in the type of paragnaths present. There is no evidence for recognition of any subspecific morphs or varieties in *Perinereis* sp. B and lesser differences (though they may still be statistically significant) can be attributed to intraspecific variation between populations.

Detailed analysis of variation and correlation in paragnath number has been carried out in a study of another species of nereidid, *Nereis diversicolor*, by Barnes & Head (1977). The statistical technique used by Barnes & Head to represent the pattern of correlations between different paragnath groups was to draw a dendrogram based on unweighted pair group averaging of the correlation coefficient matrix. This method could conceivably be taxonomically useful, however the low r values (in the range 0.11 to 0.58 for paired symmetrical groups) for *Perinereis* sp. B preclude the use of this technique. Comparable values for r from the data of Barnes & Head (1977) on *Nereis diversicolor* are in the range 0.64 to 0.74. Dendrograms of paragnath count correlation coefficients are unlikely to be taxonomically useful in nereidid taxa with levels of intraspecific variability similar to *Perinereis* sp. B.

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APPENDIX

Table 1. Enzymes examined, buffers and running conditions.

Enzyme (abbreviation; EC no.)	Running buffer	Running conditions
Adelnylate kinase (AK; 2.7.4.3)	TEB	30 m @ 300V
Aspartate amino transferase (AAT; 2.6.1.1)	TM	40 m @ 1.1mA/cm
Glucosephosphate isomerase (GPI; 5.3.1.9)	TEB	30 m @ 300V
Hexokinase (HK; 2.7.1.1)	TEB	30 m @ 300V
Isocitrate dehydrogenase (IDH; 1.1.1.42)	TM	60 m @ 1.1mA/cm
Lactate dehydrogenase (LDH; 1.1.1.27)	TM	60 m @ 1.1mA/cm
Malate dehydrogenase (MDH; 1.1.1.37)	TM	60 m @ 1.1mA/cm
Phosphoglucomutase (PGM; 2.7.5.1)	TEB	30 m @ 300V

TEB = Tris-EDTA-borate buffer pH 8.7 after Shaklee *et al.*, 1973; TM = Tris-maleate buffer pH 7.8 after Richardson *et al.*, 1980; all stain formulations after Richardson *et al.*, 1980, except HK which is after Richardson, 1983.

Table 2 Frequency of 11 alleles in samples from seven populations of the *Perinereis nuntia* complex.

Locus:	allele	Locality sample numbers						
		1	2	3	4	5	6	7
AAT:	133	–	–	–	0.03	–	–	–
	123	–	–	–	–	–	1.0	1.0
	100	1.0	1.0	1.0	0.97	1.0	–	–
AK:	100	1.0	1.0	1.0	1.0	1.0	1.0	1.0
GPI:	100	1.0	1.0	1.0	1.0	1.0	–	–
	75	–	–	–	–	–	1.0	1.0
IDH:	111	–	–	–	–	–	1.0	1.0
	100	1.0	1.0	1.0	1.0	1.0	–	–
LDH:	100	1.0	1.0	1.0	1.0	1.0	1.0	1.0
MDH:	123	–	–	–	–	–	1.0	1.0
	100	1.0	1.0	1.0	1.0	1.0	–	–

Sample sizes for each locality: 1-3, n = 10; 4, n = 30; 5, n = 2; 6, n = 4; 7, n = 3.

Table 3. Pearson product-moment correlation coefficients for numbers of paragnaths in each group on jaw length for samples from four Victorian populations of *Perinereis* sp. b.

	Apollo Bay	Separation Creek	Werribee	Flinders	all populations
I	-0.08	0.28	-0.07	-0.04	-0.01
IIL	-0.15	0.04	0.05	-0.09	-0.06
IIR	0.05	0.09	0.03	-0.17	-0.03
III	0.02	0.44**	0.27	0.20	0.12
IVLC	0.08	0.44**	0.17	0.46**	0.15
IVLB	0.12	0.31*	-0.03	0.04	0.06
IVRC	-0.13	0.29	0.24	0.42**	0.05
IVRB	0.00	0.34**	0.07	0.06	0.07
V	0.25	0.10	0.06	0.06	0.14
VIL	0.03	0.24	0.43**	0.06	0.21**
VIR	-0.03	0.33*	0.29	0.27	0.24**
VII-VIII	0.05	0.35*	0.16	0.34*	0.26**
Total Paragnaths	0.00	0.43**	0.28	0.43**	0.22**

2-tailed probabilities: * = $p < 0.01$; ** = $p < 0.001$

Table 4. Significance tests for means and variances of paragnath groups for pairwise comparisons of samples of four populations of *Perinereis* sp b.

	Means						Variances					
	A	B	C	D	E	F	A	B	C	D	E	F
I	+	+	+		+	+						+
IIL			+	+	+	+						+
IIR			+	+	+	+						+
III	+	+	+	+	+			+	+			
IVLC	+	+	+	+	+					+		
IVLB					+	+				+		
IVLT	+	+	+	+	+					+		
IVRC		+	+	+	+			+	+	+	+	+
IVRB	+			+	+		+					
IVRT		+	+	+	+			+	+	+	+	
V	+			+						+		
VIL												
VIR												
VII-VIII		+		+								

Means tested by Mann-Whitney U test (t test returned almost identical results at a higher level of significance); variances by F test. Significance level: + = $p < 0.01$. Codes for column headings: A = Apollo Bay versus Separation Creek; B = Apollo Bay versus Werribee; C = Apollo Bay versus Flinders; D = Separation Creek versus Werribee; E = Separation Creek versus Flinders; F = Werribee versus Flinders.

Table 5. Coefficients of variation (V) for numbers of paragnaths in each group for samples from four populations of *Perinereis* sp. B (V = s/Y where s is the sample standard deviation and Y is the sample mean; Sokal & Brauman, 1980).

	Apollo Bay	Separation Creek	Werribee	Flinders	all populations
I	29.63	34.15	43.04	36.29	39.07
IIL	20.54	19.84	16.93	20.36	21.55
IIR	18.09	18.09	19.76	20.05	20.43
III	18.56	17.18	15.38	16.88	20.05
IVLC	12.33	17.38	13.03	17.07	19.14
IVLB	22.63	16.88	28.32	22.24	22.95
IVLT	12.04	16.13	12.03	15.70	17.94
IVRC	19.69	19.29	11.88	16.56	21.73
IVRB	28.82	17.58	23.80	24.53	24.28
IVRT	19.11	18.17	11.29	15.14	20.42
V	34.19	48.57	26.50	37.85	37.38
VIL	11.60	11.97	11.92	11.35	11.79
VIR	10.47	11.74	12.66	10.96	11.59
VII-VIII	15.30	16.24	14.30	15.73	15.75

Table 6. Canonical loadings (correlations between conditional dependent variables and dependent canonical factors), *Perinereis* spp. A & B, samples 1 to 7.

Paragnath groups	Canonical factors 1	2
I	-0.150	**0.349**
IIL	-0.244	**0.399**
IIR	-0.261	**0.398**
III	-0.003	**0.534**
IVLC	0.035	**0.727**
IVRC	0.024	**0.633**
V	-0.064	0.022
VIL	**0.300**	-0.108
VIR	**0.283**	-0.128
VIIVIII	**-0.640**	0.076

(figures in bold are discussed in the text)

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A Revision of the *Perinereis nuntia* Species Group (Polychaeta: Nereididae)

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ABSTRACT. The *Perinereis nuntia* species group is revised on the basis of material from worldwide localities. Twenty available names are reduced to 12 recognised species, including two new species: *Perinereis akuna* (from southern Australia) and *P. namibia* (from southern Africa). Specimens from Indonesia and from Juan Fernandez Islands cannot be identified and may represent two additional undescribed species. *Perinereis broomensis* Hartmann-Schröder, 1979 is synonymised with *P. nuntia* (Savigny, 1818) for the first time. A key to species is provided.

WILSON, R.S. & C.J. GLASBY, 1993. A revision of the *Perinereis nuntia* species group (Polychaeta: Nereididae). Records of the Australian Museum 45(3): 253–277.

The *Perinereis nuntia* species group is characterised by an arc of bar-shaped paragnaths on Area VI of the eversible proboscis. These nereidid worms are common in intertidal and shallow marine waters and are widely distributed on the coasts of the southern continents and the tropical Indo-Pacific (Fig.1). Wilson (1993) studied two unidentified species in the *P. nuntia* species group from southeastern Australia and provided guidelines for the interpretation of morphological variability. In this paper we apply the results of Wilson (1993) to a worldwide revision of the *Perinereis nuntia* species group. The remaining species in the genus *Perinereis* have been treated by Hutchings *et al.* (1991).

Perinereis nuntia (Savigny, 1818) was described from the Gulf of Suez. There are few subsequent published records until the radical treatment of Fauvel (1932), who synonymised *P. nuntia* with a number of species previously regarded as distinct. Most recent authors have followed Fauvel, and *P. nuntia* has now been recorded from all southern hemisphere continents except Antarctica, from Japan through South-east Asia to India and the Middle-East. Fauvel's influence has also resulted in the widespread adoption of trinomens in an attempt to account for morphological variability in this supposed species. Fauvel's trinomens apparently were not intended to represent geographical variants or subspecies since each was credited with a wide distribution and several varieties were often recorded from the same locality or region. Fauvel (1932: 109) observed that "Between the varieties of this unsettled species many specimens are intermediate, and so gradual are the transitions that they cannot be assigned definitely to any variety". Trinomens continue to be widely used in the literature for this species group, which includes 20 nominal species and

varieties (Table 1). Wilson (1993) could not recognise subspecific taxa in this group in a study of seven populations in southeastern Australia, but there has been no attempt to revise the taxonomy of the group globally.

Materials and Methods

Collections representing about 50 populations from throughout the range of the *Perinereis nuntia* group were examined (Fig.1). Paragnaths were counted for all Areas and qualitative differences in paragnath type and setal distributions were also recorded (see Wilson, 1993 for a descriptions of morphological methods and terminology). Body length and width, and jaw length measurements were recorded in mm; jaw length was used as a size measure for morphometric purposes (following Wilson, 1993). Width measurements refer to the body width at setiger 10 and (where the condition of the specimen permits) is given as two figures, the first excluding parapodia, the second (in parentheses) including parapodia but excluding setae. Use of the terms anterior and posterior in descriptions of the relative positions of paragnaths apply to the fully everted proboscis, with the maxillae in the anterior-most position (as drawn in Fig.12a,b). Systat version 4.0 (Wilkinson, 1988) running on an MS-DOS personal computer was used for all statistical analyses.

Institutions from which material was borrowed are referred to in the text by the following codes: AM – Australian Museum, Sydney, Australia; HZM – Zoological Institute and Museum, Hamburg University, Hamburg, Germany; MNHN – National Museum of Natural History, Paris, France; NMV – Museum of Victoria, Melbourne, Australia; NMW – National Museum of Wales, Cardiff, Wales; NR – collection of N. Rozbaczylo, Pontificia Universidad Catolica de Chile, Santiago, Chile; NTM – Northern Territory Museum and Art Gallery, Darwin, Australia; PMBC – Phuket Marine Biological Center, Phuket, Thailand; QM – Queensland Museum, Brisbane, Australia; SAMA – South Australian Museum, Adelaide, Australia; SAMC – South African Museum, Cape Town, South Africa; SRP – collection of Sun Ruiping, Institute of Oceanology, Academia Sinica, Qingdao, Peoples Republic of China; USNM – United States National Museum, Washington, USA; WAM – Western Australian Museum, Perth, Australia; WMP – Wroclaw Museum, Wroclaw, Poland; ZMA – Zoological Museum, Amsterdam, The Netherlands; ZMB – Zoological Museum, Berlin, Germany; ZMK – Zoological Museum, Copenhagen, Denmark.

Tables are listed in the Appendix.

Statistical Analysis

In this paper we apply canonical variates analysis (CVA, otherwise known as multiple discriminant analysis) to the problem of species identifications among numerous populations of closely related worms from around the world. The characters used in the CVA were paragnath counts for each area of the proboscis. Canonical variates analysis requires *a priori* groupings of specimens, however these groupings can be at the level of local populations. Subsequent recognition of a smaller number of clusters in the final analysis is an exploratory technique described by Wiley (1981: 361-365). This use of CVA as a clustering technique as an aid to species determinations is an extension of the approach of Wilson (1993), who used CVA to cluster

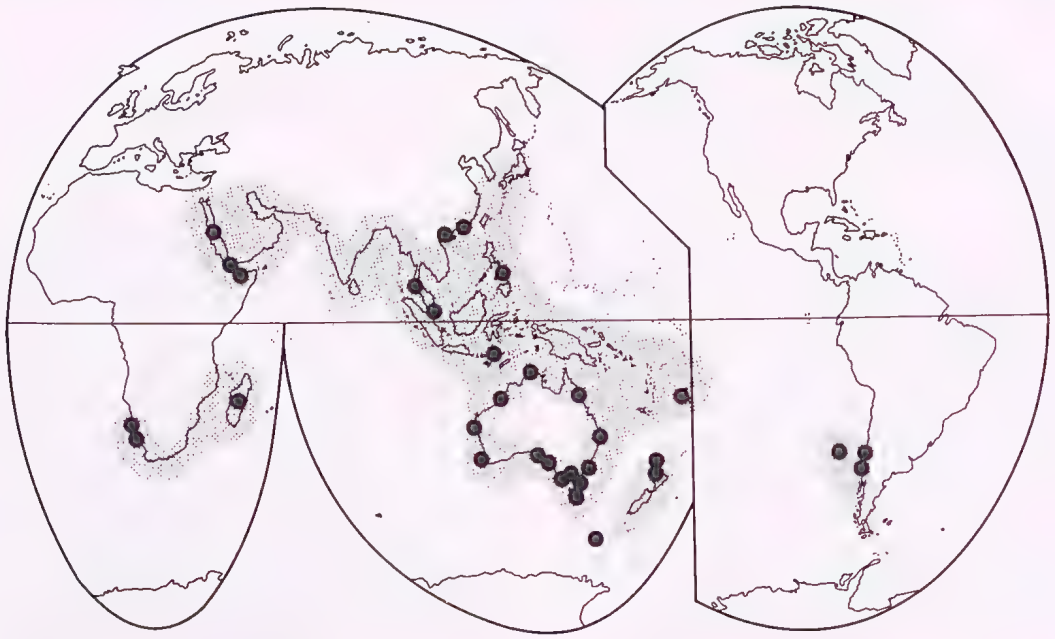

Fig.1. Distribution map of range of *Perinereis nuntia* species group (stippled area), and localities for collections used in this study (filled dots).

populations into two species that had been independently distinguished using electrophoresis.

The validity of canonical variates analysis depends on normality of the data and homogeneity of variances. These assumptions were tested for the two most numerous species: *Perinereis nuntia* and *P. vallata*. Departures from normality were checked by probability plots of cumulative percent-frequencies (as recommended by Reyment *et al.*, 1984), homogeneity of variances was tested by F-tests. Using these methods Area I and V paragnath counts for some samples appeared to be non-normal and/or have heterogeneous variances. However, omitting these variables had little effect on the results of preliminary analyses. Reyment *et al.* (1984) note that multivariate methods such as CVA appear to be reasonably robust to departures from normality and analyses were performed with all variables included.

It is also necessary to exclude (or allow for) the possibility that differences between populations might be size-related. Wilson (1993) concluded that size-dependent variation in paragnath counts was not significant. This result was confirmed in this study; calculation of coefficients of determination (r) shows that variation in size accounts for only 7.5% of the total variation in paragnath counts in *P. nuntia* and 9.0% in *P. vallata*. We also needed to be confident that each local population sample comprised only one species. Within samples there were no qualitative differences and frequency distributions of paragnath counts for each area of the proboscis appeared to be unimodal. We therefore conclude that each sample contains a single species.

Fifty local population samples were available for analysis. Qualitative differences were immediately apparent among the specimens and were used to distinguish smaller data sets for CVA. Two taxa were distinguished by additional bands of numerous, minute paragnaths on Areas VII-VIII. Frequency distributions of paragnath counts in each Area appeared to be unimodal and these species are identified in the systematic account as *Perinereis akuna* n.sp. (= *Perinereis* sp. A of Wilson, 1993) and *P. rhombodonta* Wu, Sun & Yang, 1981. A third series of samples was distinguished by an indented prostomium, the absence of paragnaths from Areas I and II, novel arrangements of paragnaths on Areas V and VI, and bar-shaped paragnaths on Area VI arranged stepwise (rather than in an even line or arc as in all other species described here). This material was also excluded from the statistical analysis and is identified below as *P. caeruleis* (Hoagland, 1920).

The remaining material, representing the bulk of the collection, was divided into two groups distinguished by the presence or absence of smooth, parallel bar-shaped paragnaths on Area IV of the proboscis (Wilson, 1993: fig.7). This new character seemed to be taxonomically useful for two reasons: (i) presence/absence of bars on Area IV showed almost no variation within samples (the only minor exception being three specimens of *Perinereis namibia* n.sp.; see below); (ii) among related genera, many species also have bars on Area IV (*Neanthes*, *Ceratonereis sensu lato*; Wilson, 1984, unpublished data). Other genera contain no known

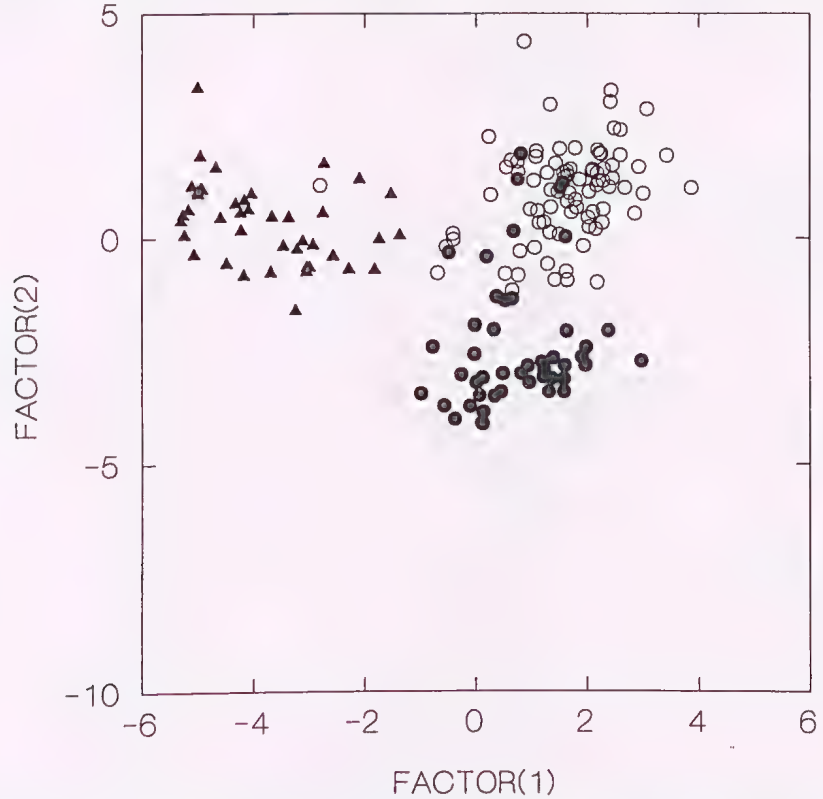

Fig.2. Canonical variates analysis, scatter plot, *Perinereis nuntia* group, material lacking bars on Area IV, factor(2) versus factor(1). Filled circles = *P. nuntia* (Red Sea); open circles = *P. nuntia* (Indo-Pacific); filled triangles = *P. namibia*.

species with bars on Area IV (*Nereis*, *Platynereis*; Wilson, 1985). Thus, presence or absence of bars on Area IV may be useful at a higher taxonomic level.

Species lacking bars on Area IV. Worms lacking parallel bars on Area IV came from samples from the Red Sea, South Africa, South-east Asia, northern Australia, China, Hong Kong and Fiji. Canonical variates analysis clustered the 14 samples into two clusters. Examination of locality data showed that the clusters represent geographically separate populations and are recognised in the descriptions below as *Perinereis namibia* n.sp. and *P. nuntia* (Savigny, 1818). The results of the CVA are presented as a plot of factor scores for each canonical variate. Canonical loadings for Factor 1 indicate that paragnath counts for Area VII-VIII best discriminate the two species (Table 2). There is some separation of populations of *P. nuntia* from the Red Sea from populations from the Indo-Pacific by Factor 2 scores, however the level of separation is comparable to that seen between conspecific populations of *Perinereis* sp. B by Wilson (1993). There are no discernable differences in parapodia or other taxonomic characters among these specimens, all of which we refer to a single species. Factor 3 scores do not provide any additional separation of taxa and are not plotted here. Factors 1 to 3 cumulatively account for 92% of the total variation; Factors 1 and 2 account for 86%. Frequency distributions of paragnath counts that showed the highest loadings for Factors 1 and 2 are provided in Figure 3.

Since CVA maximises the separation between groups compared with the variation within groups, this technique is inappropriate for attempting to discriminate samples comprised of few specimens. Three populations were represented by samples of only one or two specimens: *Perinereis ponuiensis* Augener, 1927, *P. rumphii* Horst, 1919 and *Perinereis* sp. 1 (from Juan Fernandez Islands). These samples were retained in the CVA in the hope that their affinities would be indicated by the canonical variates analysis. *Perinereis ponuiensis* is provisionally retained as a distinct species, *P. rumphii* is synonymised with *P. nuntia*, and *Perinereis* sp. 1 remains unidentified and may represent an undescribed species. These decisions are justified in the Remarks section under each species.

Species with bars on Area IV. Parallel bars on Area IV were present in samples from Madagascar, southern Australia, New Zealand, Macquarie Island and Chile.

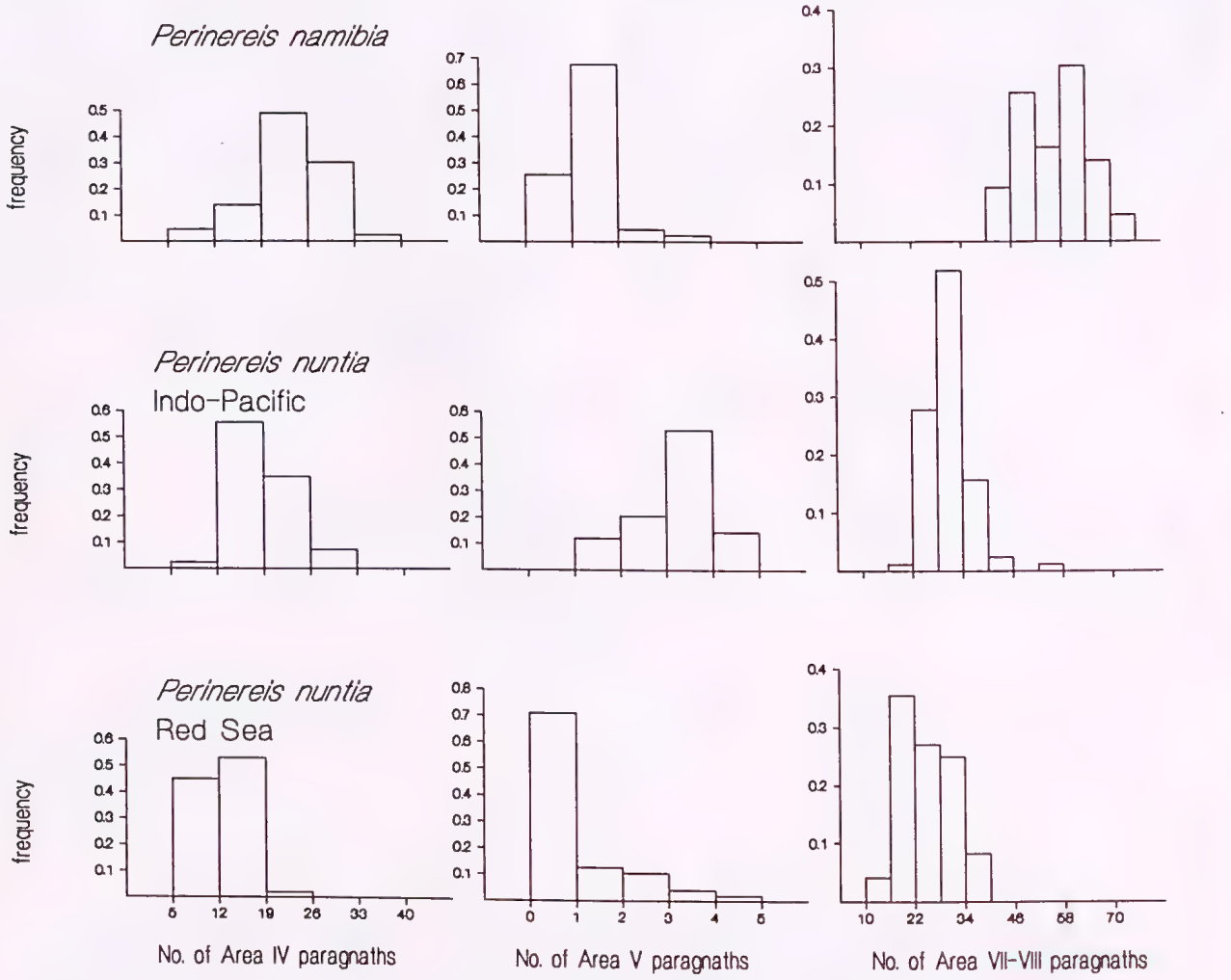

Fig.3. Frequency distributions, species lacking bars on Area IV; Area IV, V and VII-VIII paragnath counts.

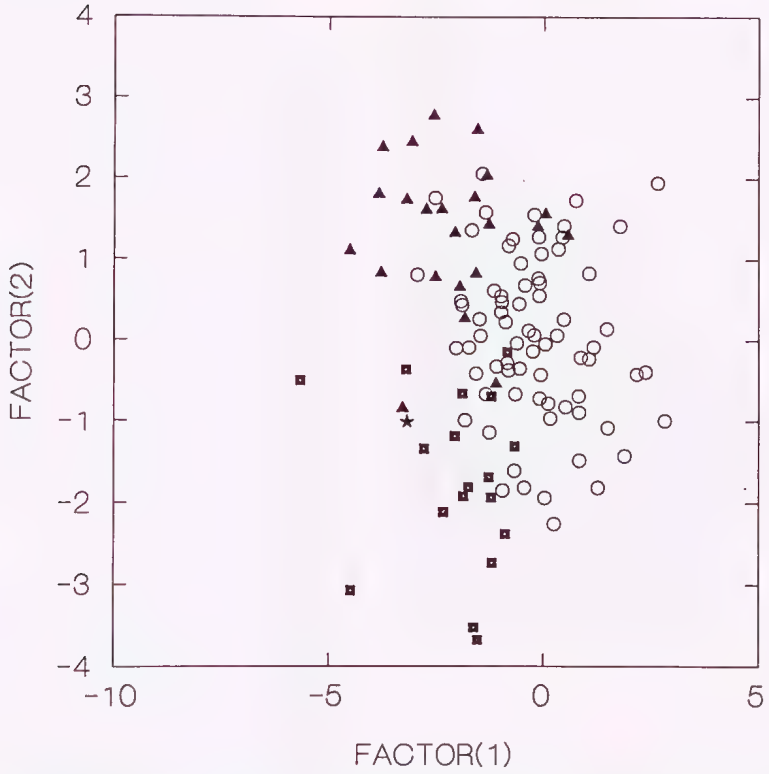

Fig.4. Canonical variates analysis, scatter plot, *Perinereis vallata* samples, factor(2) versus factor(1). Open circles = *P. vallata* (Australia); filled squares = *P. vallata* (Chile); filled triangles = *P. vallata* (New Zealand); star = *Perinereis* sp. (Indonesia).

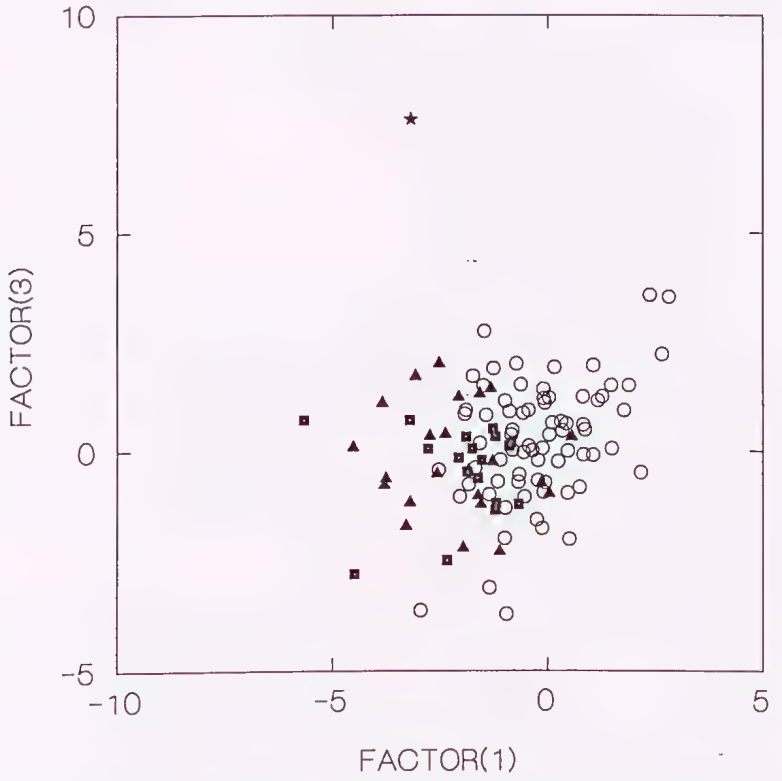

Fig.5. Canonical variates analysis, scatter plot, *Perinereis vallata* samples, factor(3) versus factor(1). Open circles = *P. vallata* (Australia); filled squares = *P. vallata* (Chile); filled triangles = *P. vallata* (New Zealand); star = *Perinereis* sp. (Indonesia).

Among this material, *Perinereis akuna* n.sp. has already been distinguished (as *Perinereis* sp. A) by Wilson (1993). The remaining material showed no qualitative differences and was subjected to CVA, resulting in a single specimen from Madagascar (identified below as *Perinereis majungaensis*) being plotted as distinct from all other material. Outliers compress the scale on which remaining groups may be distinguished. If this outlier is excluded and the data re-analysed no distinct clusters of specimens can be recognised (canonical loadings are presented in Table 3). There is some separation of samples from Australia, New Zealand and Chile on Factors 1 and 2 (Fig.4), but the level of separation of populations and the similarity of percent-frequency histograms of paragnath counts (Fig.6) are comparable to that seen in five conspecific populations of *Perinereis* sp. B (Wilson, 1993). We do not feel justified in recognising more than one species among this material, which is identified below as *Perinereis vallata*. The identity of a single specimen from Indonesia remains equivocal; this specimen is separated by Factor 3 scores (Fig.5) and is discussed below as *Perinereis* sp. 2.

Descriptive statistics for all of these species are provided in Table 4.

Systematic Account

The following is a list of all species described here:

P. akuna n.sp.
P. caeruleis (Hoagland, 1920)
P. gualpensis Jeldes, 1963*
P. maindroni Fauvel, 1943
P. majungaensis Fauvel, 1921
P. matthaii Aziz, 1938*
P. mictodonta (Marenzeller, 1879)*
P. namibia n.sp.
P. nuntia (Savigny, 1818)
P. ponuiensis Augener, 1927
P. rhombodonta Wu, Sun & Yang, 1981
P. vallata (Grube, 1858)
Perinereis sp. 1 [Juan Fernandez]
Perinereis sp. 2 [Indonesia]

(We have not been able to examine material of those species marked with an asterisk.)

The *Perinereis nuntia* group can be diagnosed and described as follows. Species descriptions do not repeat this information.

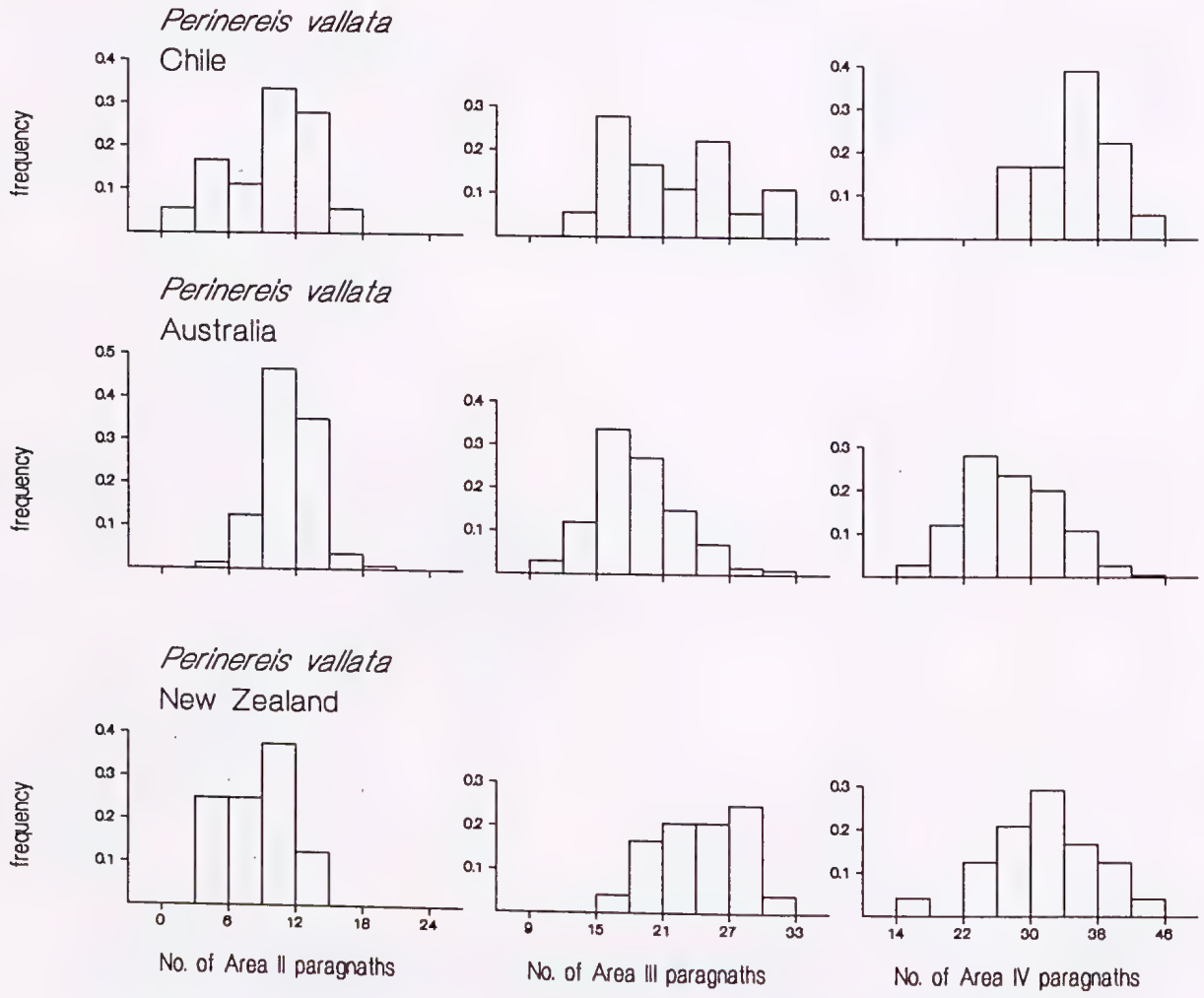

Fig.6. Frequency distributions, *Perinereis vallata* samples, Areas II, III and IV paragnath counts.

Perinereis nuntia Species Group

Diagnosis. Nereidids with eversible pharynx with conical paragnaths on both rings. Area VI with 3-20 bar-shaped paragnaths or a mixture of bars and cones on each side in a single line or arc. Notosetae homogomph spinigers. Superior notopodial lobe similar in length to inferior notopodial lobe throughout (in atokes).

Description. One pair of biarticulate palps, 1 pair of antennae. Two pairs of eyes, anterior pair more widely spaced than posterior pair. Four pairs of tentacular cirri. Eversible pharynx with 1 pair of jaws. Paragnaths on Area VI bars only or bars and cones. Paragnaths on Area IV cones only or bars and cones. All other Areas with conical paragnaths only. Range of paragnaths observed for each Area: I = 0-9; II = 0-64; III = 2-185 (1 or several almost invariably located in distinct lateral patches); IV = 0-131 cones and 0-13 bars; V = 0-5; VI = 3-20 bars; VII-VIII = 10-250, sometimes including numerous minute cones in a distinct band (posterior when pharynx everted). One pair of ventrally attached anal cirri. Parapodia 1 and 2 lack notosetae, thereafter all parapodia biramous. Notopodia bilobed from setiger 3, superior lobe not expanded or significantly longer than inferior lobe on posterior setigers (in atokes). Dorsal cirrus basally attached to notopodia. Neuropodia bilobed throughout, with ventral cirrus. Notosetae homogomph spinigers. Neurosetae homogomph spinigers and heterogomph falcigers in the dorsal fascicle, heterogomph spinigers and heterogomph falcigers in the ventral fascicle (heterogomph spinigers sometimes absent).

Perinereis akuna n.sp.

Fig.7a-m

Perinereis sp. A Wilson, 1993: 248, fig.7A.

Type material examined. HOLOTYPE: Australia: New South Wales: Coal & Candle Creek, Hawkesbury River, near Akuna Bay, 33°37'S 151°14'E, intertidal under stones in sandy mud, coll. P.A. Hutchings & R.S. Wilson, 19 Oct. 1986, NMV F53985. PARATYPES: same data as holotype, NMV F53986, F53987, 2 paratypes, AM W21385-W21386, 2 paratypes; New South Wales: Batemans Bay, Clyde River, north shore under Princess Highway bridge, intertidal, under stones in muddy shell, coll. R.S. Wilson, 17 July 1987, NMV F53988-53994, 7 paratypes.

Additional material examined. WESTERN AUSTRALIA: Trigg, reef platform, coll. F. Wells, 21 Jan. 1987, AM W202973. SOUTH AUSTRALIA: Sellicks Beach, 14 Mar. 1985, sandy algal turf on limestone platform, intertidal, G.C.B. Poore & H.M Lew Ton (NMV station SA 4), NMV F53996, 1 specimen. NEW SOUTH WALES: Fisheries Creek, Twofold Bay, among oysters, coll. S. Keable & E. Bamber, 12 Dec. 1984, AM W202969, 13 specimens; Fisheries Creek, Twofold Bay, intertidal mud, coll. S. Keable, AM W202976, 7 specimens; Nullica River estuary, Twofold Bay, mud & *Zostera* sievings, coll. S. Keable & P. Hutchings, 18 Sept. 1986, AM W203008, 1 specimen; Nullica River estuary, Twofold Bay, intertidal rock fauna, coll. S. Keable & P. Hutchings, AM W203009, 2 specimens; Merimbula, 150 m from mouth of Back Lake, soft sandstone reef, coll. J.H. Day *et al.*, 23 July 1975, AM W15769, 3 specimens; Batemans Bay, from oysters, 31 Dec. 1969, NMV F53995, 1 specimen; Port Hacking, upper south-west arm, coll. V. Wadley, WAM 15-85, 8 male epitokes; Port Hacking, 6 month settlement plate, 1-2 m, coll. R. Fisher, CSIRO, 21 Dec. 1974, AM W202975, 3 specimens; Woollahra Point, AM W202920, 1 specimen; Botany Bay, 1910, AM W181, 2 specimens; Rushcutters Bay, AM W4786, 1 female epitoke; Spit Bridge marina, Middle Harbour, Sydney, on pilings among barnacles, coll. N. Tait, 29 June 1972, AM W203010, 1 specimen; Port Jackson, AM W4843, 2 specimens; Broken Bay, AM W4841, 1 specimen; Lake Macquarie, 17 July 1953, AM W4838, 1 specimen; north of Coffs Harbour, in sand, 23 Mar. 1972, coll. P. Hutchings, AM W202923, 1 specimen; Point Hastings, east of Murwillumbah, LWM, on sheltered rocks & oysters, coll. I. Loch, 26 Oct. 1976, AM W203011, 2 specimens; Wooli, among oysters on rocks, coll. P. Hutchings, 25 Feb. 1971, AM W203012, 1 specimen. QUEENSLAND: Picnic Cove, Noosa Heads, on loose rocks, semi-sheltered, coll. I. Loch, 21 Oct. 1976, AM W202970, 1 specimen; Middle Banks, Moreton Bay, Nov. 1983-Nov. 1984, P. Saenger & S. Cook, QM GH4028, 1 specimen; Calliope River, Gladstone, coll. P. Saenger, 1974-1983, AM W199377, 1 specimen; Barnes Creek, Mackay, 3 km upstream from mouth, coll. Turner *et al.*, 24 Sept. 1970, AM W203092, 1 specimen.

Description. Type series comprises 12 specimens, size range 18 setigers (anterior fragment), length 5 mm, width 1(1.5) mm, jaw length 0.9 mm to 30 setigers (anterior fragment), length 20 mm, width 2.5(4.5) mm, jaw length 2.5 mm. Median longitudinal band present, width half that of body, of slightly darker brown pigmentation on dorsum of anteriormost 10-15 setigers; entire prostomium and dorsal peristomium also darker. Eyes dark blue/black, subdermal. Length of prostomium equal to width. Antennae one-third as long as prostomium. Tentacular cirri extend back 7-8 setigers. Jaws thin, transparent brown in small specimens, heavier and opaque in larger specimens, always with 5-7 distinct teeth. Paragnaths: I = 2-4; II = 14-26; III = 14-26 (distinct lateral groups present); IV = 15-37 cones, and 2-4 bars; V = 1-4; VI = 6-11 bars; VII-VIII = 42-55 large cones in 2 rows, and 54-141 small cones in a distinct band posterior to the larger paragnaths. Anal cirri as long as posteriormost 7-8 setigers.

Notopodia with 2 similar conical lobes from setiger 2, and basally inserted dorsal cirri of equal length. Small but distinct digitiform presetal lobe present at base of inferior notopodial lobe on setigers 5-30, largest on setigers 10-20. Neuropodia with 2 lobes, dorsal lobe more rounded and shorter throughout, ventral lobe more acute and similar in shape and length to notopodial lobes. Ventral cirri about three-quarters length of ventral neuropodial lobe and basally inserted. All parapodial lobes more slender on posterior setigers but proportions otherwise similar throughout. Neuropodial heterogomph spinigers present throughout.

Remarks. *Perinereis akuna* can be distinguished from all other species in the *Perinereis nuntia* species group by the additional band of minute paragnaths in the posteriormost part of VII-VIII. *Perinereis akuna* occurs in similar habitats and within the range of *P. vallata* in southern Australia; these species can also be separated by paragnath counts for Areas II and VI (Table 4). Wilson (1993) showed that *P. akuna* and *P. vallata* are also distinguished by fixed allelic differences at four enzyme loci.

Etymology. The specific name *akuna* is derived from an Australian aboriginal word now used as a place name near the type locality. It is to be treated as indeclinable.

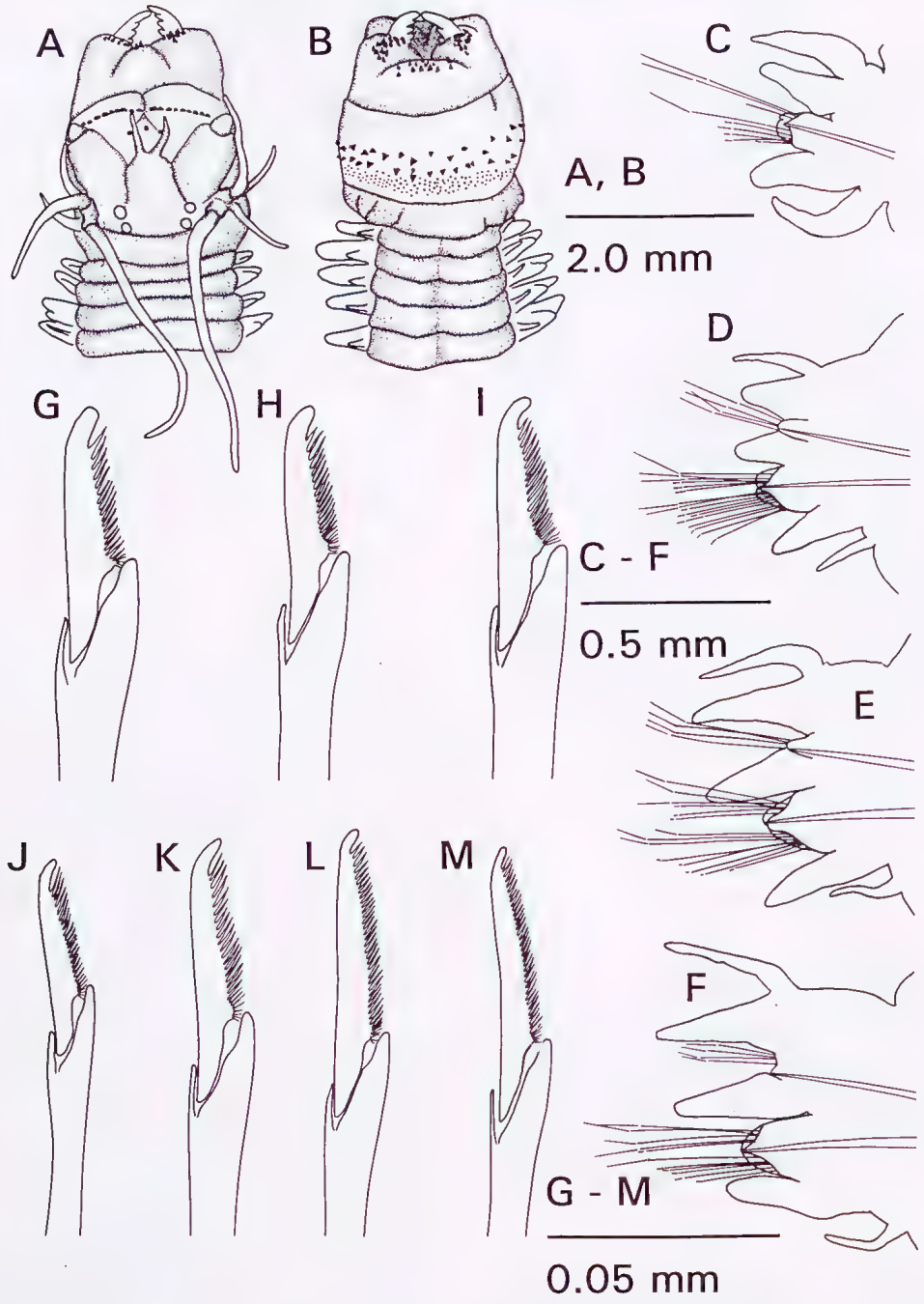

Fig.7. *Perinereis akuna* n.sp. New South Wales: Coal & Candle Creek, Hawkesbury River, 19 Oct. 1986, NMV F53985, holotype: A – extended proboscis, dorsal view; B – extended proboscis, ventral view. New South Wales: Batemans Bay, Clyde River, 17 July 1987, NMV F53988, C – setiger 1 parapodium, anterior view; D – setiger 10 parapodium, anterior view; E – setiger 50 parapodium, anterior view; F – setiger 87 parapodium, anterior view; G – heterogomph falciger, dorsal neuropodial fascicle, setiger 10; H – heterogomph falciger, dorsal neuropodial fascicle, setiger 57; I – heterogomph falciger, dorsal neuropodial fascicle, setiger 87; J – heterogomph falciger, ventral neuropodial fascicle, setiger 1; K – heterogomph falciger, ventral neuropodial fascicle, setiger 10; L – heterogomph falciger, ventral neuropodial fascicle, setiger 50; M – heterogomph falciger, ventral neuropodial fascicle, setiger 87.

Distribution. Widespread in south-eastern Australia from Gladstone in the north to Twofold Bay in the south. Two isolated records from South Australia and south-western Western Australia. Collected on a variety of hard substrates, including cobble, but apparently restricted to the intertidal zone and can occur in areas of reduced salinity.

Perinereis caeruleis (Hoagland, 1920)

Fig.8a-n

Nereis (Heteronereis) caeruleis Hoagland, 1920: 608-610, pl.47 figs 13-16, pl.48 figs 1-4.

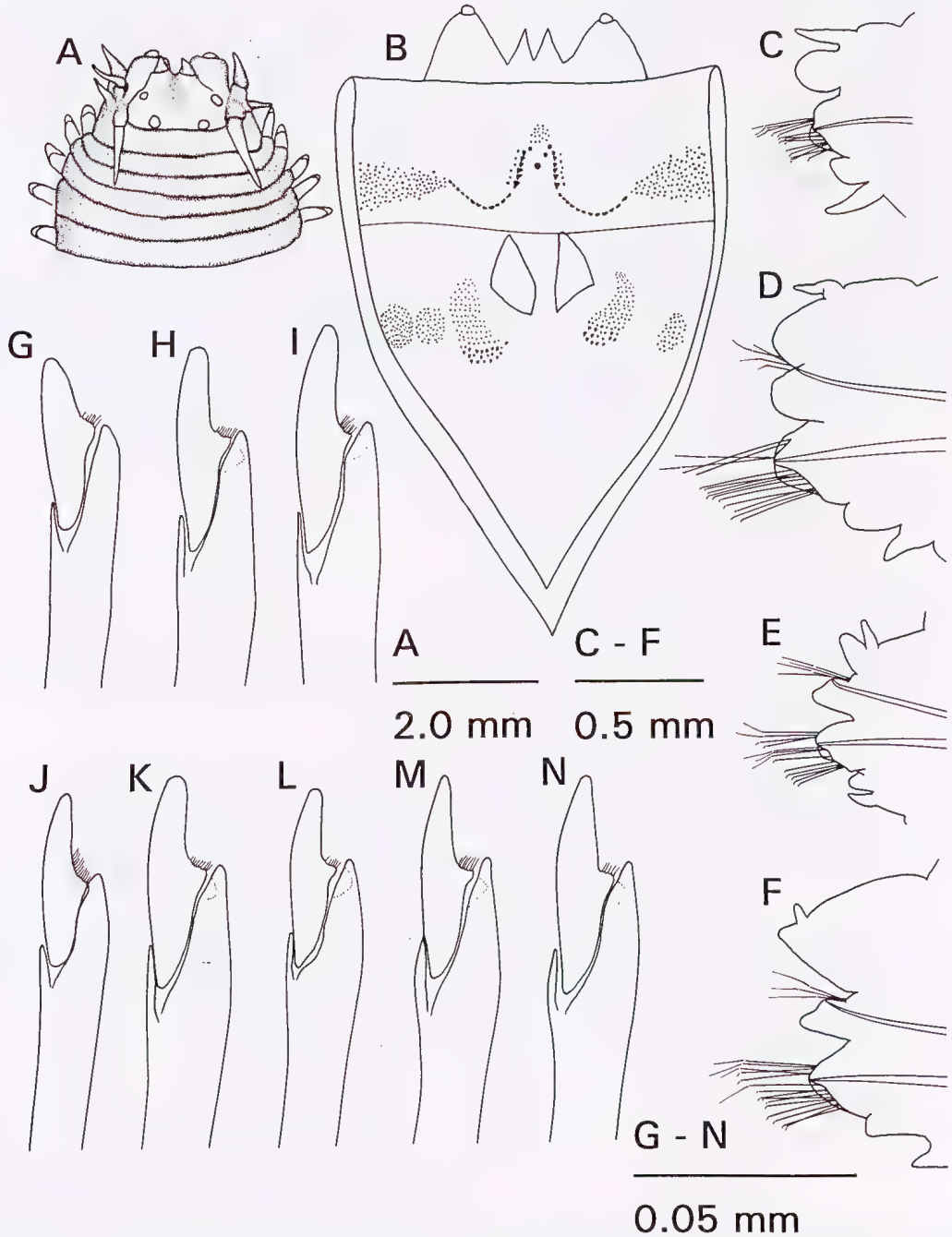

Fig.8. *Perinereis caeruleis* (Hoagland, 1920). Northern Territory: Annersley Point, 16 June 1984, NTM W1806: A – dorsal view of head; B – schematic ventral view of dissected proboscis (not to scale); C – setiger 1 parapodium, anterior view; D – setiger 10 parapodium, anterior view; E – setiger 50 parapodium, anterior view; F – setiger 237 parapodium, anterior view; G – heterogomph falciger, dorsal neuropodial fascicle, setiger 1; H – heterogomph falciger, dorsal neuropodial fascicle, setiger 10; I – heterogomph falciger, dorsal neuropodial fascicle, setiger 50; J – heterogomph falciger, ventral neuropodial fascicle, setiger 1; K – heterogomph falciger, ventral neuropodial fascicle, setiger 10; L – heterogomph falciger, ventral neuropodial fascicle, setiger 50; M – heterogomph falciger, ventral neuropodial fascicle, setiger 120; N – heterogomph falciger, ventral neuropodial fascicle, setiger 237.

Material examined. AUSTRALIA: Northern Territory: Annersley Point, mangrove at base of cliff, Malay Bay Road, intertidal, coll. R. Hanley *et al.*, 19 June 1984, NTM W1772, 5 specimens. Annersley Point, Stn AP1, rock shelf along sandy beach, intertidal, coll. R. Hanley *et al.*, 16 June 1984, NTM W1806, W1811, 4 specimens.

PHILIPPINES: Limbe Strait, coll. "Albatross", 9 Nov. 1909, USNM 18948, holotype.

NEW HEBRIDES: coll. Kawalcasky, MNHN, 1 male epitoke (specimen from P. Fauvel collection, labelled *P. neocaledonica*).

Description. Based on 9 Australian specimens, size range 69 setigers (anterior fragment), length 18 mm, width 1.4(3.4) mm, jaw length 1.4 mm to 313 setigers (entire specimen), length 90 mm, width 2.2(4.5) mm, jaw length 2.1 mm. Pigmentation dark brown on prostomium and anterior dorsum, with prominent darker median longitudinal stripe. Pigmentation posteriorly lighter, limited to mid-dorsal longitudinal stripe. Eyes black. Length of prostomium three-quarters times width. Anterior margin of prostomium indented to a distance equal to half the length of the antennae in some specimens, others with little or no indentation. A prominent circular depression present in anterior prostomium between antennae. Antennae one-third as long as prostomium. Tentacular cirri extend back 2-4 setigers. Jaws heavy, dark brown, with no teeth. Paragnaths: I = 0-2; II = 0; III = 60-90 in a central group, plus 2 distinct lateral groups each of 30-40; IV = 80-100 cones, bars absent; V = 1-4 large cones plus 20-40 small cones posterior to the larger cones; VI = 8-17 bars plus 7-20 cones in distinct patches close to Area V; VII-VIII = about 200-250 very small cones, plus 3-4 large cones on each side close to Area VI. Anal cirri as long as posteriormost 4 setigers.

Parapodia of setigers 1 and 2 directed anteriorly. Anterior notopodia with 2 equal lobes and basally attached dorsal cirrus of equal length. Dorsal notopodial lobe becoming expanded from median setigers, up to twice as long as ventral lobe and with distally attached dorsal cirrus. Anterior neuropodia with 2 unequal lobes, ventral lobe about half as long as dorsal lobe. Median and posterior neuropodia with ventral lobe reduced to a small protuberance on ventral margin of superior neuropodial lobe. Ventral cirri one-quarter as long as superior neuropodial lobe throughout. Neuropodial falcigers with distal portion of blade shorter than proximal (articulated) region (Fig.8g-n). Neuropodial heterogomph spinigers absent from anteriormost 24-35 setigers.

Remarks. The holotype is an epitoke and closely fits the original description of Hoagland (1920). The proboscis and head are in poor condition, nevertheless, there are no significant differences between the holotype and the Australian material.

Perinereis caeruleis differs from all other species described in this paper by having a variably indented prostomium; paragnaths absent from II (and usually from I also); additional groups of paragnaths present on V and VI; and distinctive short-bladed falcigers.

Perinereis neocaledonica Pruvot, 1930 is closely related to *P. caeruleis* and may be a junior synonym. Fauvel (1932) noted that *P. caeruleis* differs from *P. neocaledonica* in having a "normal" Area I (ie, paragnaths present), however the material examined here is variable in this respect. A male epitoke labelled *P. neocaledonica* from Fauvel's collection and collected in the New Hebrides differs in having more numerous small paragnaths on VI (patches of about 40 on each side) and VII-VIII (approximately 380) than the type material of *P. caeruleis* and the material of *P. caeruleis* from northern Australia. Examination of the type material and additional collections from the region of New Caledonia will be required to determine if the South Pacific contains an additional species that should be called *P. neocaledonica*.

Distribution. *Perinereis caeruleis* was previously known only from the Philippines. The material from Annersley Point, near Darwin, represents the first record of *P. caeruleis* from Australia. *Perinereis neocaledonica* is recorded from the Arabian Sea (Fauvel, 1932), Taiwan (Wu, 1967), southern Japan (Imajima *et al.*, 1985), as well as from New Caledonia (Pruvot, 1930; Rullier, 1972) and the New Hebrides (material examined above).

Perinereis gualpensis Jeldes, 1963

Perinereis gualpensis Jeldes, 1963: 3-10.–Rozbaczylo & Castilla, 1973: 220.–Bertrán, 1980: 82-83, fig.1.–Jaramillo *et al.*, 1984: 124,127.

Description (taken from Bertrán, 1980). Paragnaths: I = 0-7; II = 6-17; III = 24-48; IV = 18-39 cones; V = 1-2; VI = 6-11 bars; VII-VIII = 30-47 large cones. Notopodia with 2 equal conical lobes, and digitiform presetal lobe on anterior setigers back to at least setiger 28. Dorsal notopodial lobe not expanded on posterior setigers, dorsal cirrus about as long as dorsal notopodial lobe and basally inserted throughout. Neuropodia with similar lobes throughout, and ventral cirrus about three-quarters as long as neuropodial lobes. Neuropodial heterogomph spinigers are present.

Remarks. We have not been able to examine type material, which is in poor condition (Rozbaczylo & Castilla, 1973). Bertrán (1980) has shown that *P. gualpensis* is similar to Chilean populations of *P. vallata* but differs in having longer antennae, lacking lateral groups on Area III, and having fewer paragnaths on VI than the latter species. The morphometric relationship between number of segments and body length also separates the two species. *Perinereis gualpensis* occurs in estuarine regions subject to more freshwater influence and salinity fluctuations than *P. vallata* (Bertrán, 1980).

Distribution. *Perinereis gualpensis* is known only

from three estuaries in Chile, from fresh and brackish water.

Perinereis maindroni Fauvel, 1943

Fig.9a-g

Perinereis maindroni Fauvel, 1943: 201-202, fig.1e-i.–Fauvel, 1953: 203-204, fig.104e-i.

Material examined. India: Pondicherry, coll. M. Maindron, 1901, MNHN, 1 SYNTYPE.

Description. Size: 50 setigers (entire), length 17 mm, width 1.0(1.6) mm, jaw length not recorded. Peristomium orange-brown, slightly darker than prostomium and setigerous segments, otherwise no pigmentation. Eyes dark red. Prostomium as long as wide, antennae half as long as prostomium. Tentacular cirri extend back 0 (shortest) to 3+ setigers (longest tentacular cirri are broken). Jaws translucent brown, with about 5 teeth. Paragnaths minute translucent orange: I = 0; II = 8, 6; III = 8 (distinct lateral groups not visible); IV = 8, 8 cones, bars absent; V = 1 cone exactly at the apex of VI left & right; VI = 6, 6 evenly spaced bars; VII-VIII 35 in about 2 rows, no additional separate bands of small cones. Anal cirri ventrally inserted, as long as posteriormost 10 setigers.

Notopodia of setigers 1 and 2 with 2 equal triangular lobes, setigers 3-20 with 3 equal triangular lobes, and basally inserted dorsal cirri of similar length. Digitiform presetal lobe absent. Anterior neuropodia with rounded dorsal lobe and acute ventral lobe from setiger 3. Neuropodial lobes equal in length on anterior setigers but dorsal lobe reduced to about half length of ventral lobe by about setiger 20-25. Digitiform postsetal neuropodial lobe present from about setiger 15, initially about half as long as ventral lobe, becoming equal in length to ventral lobe (but narrower) by setigers 20-25. Ventral cirri about as long as ventral neuropodial lobe throughout and basally inserted. Notopodia from setiger 21 with narrow elongate superior lobe becoming 2-3 times as long as ventral lobe on about setigers 25-35. Median notopodial lobe reduced to small presetal lobe

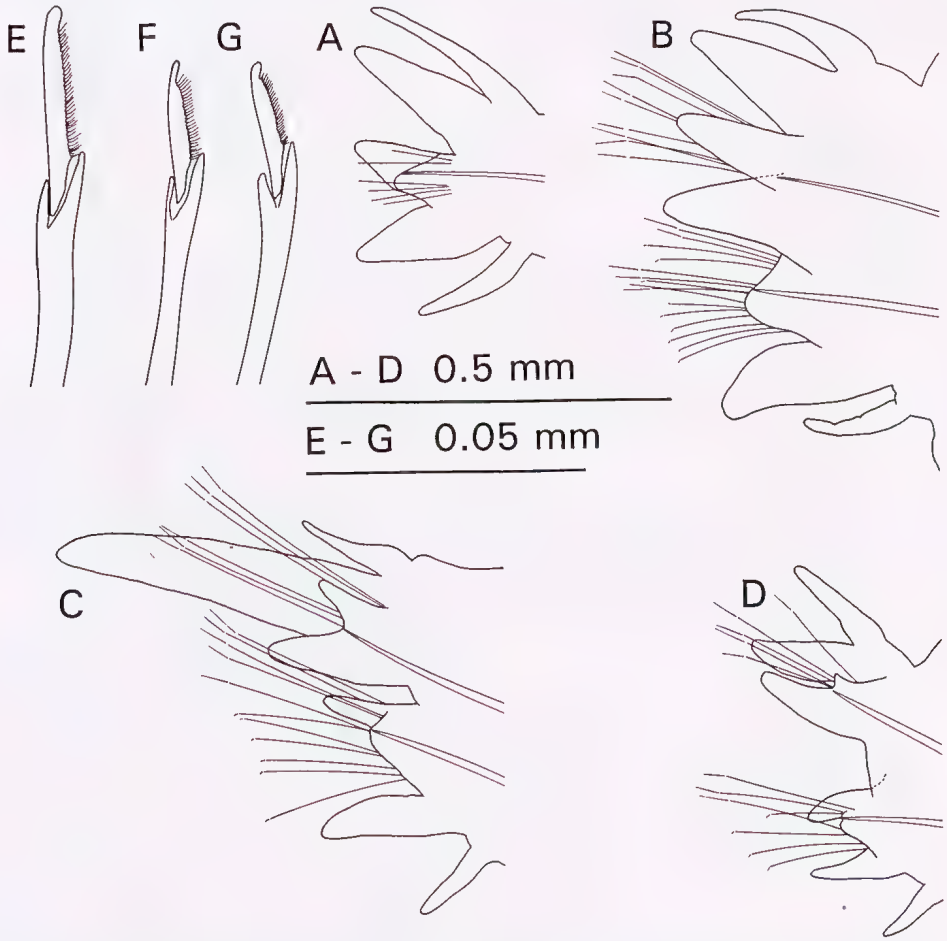

Fig.9. *Perinereis maindroni* Fauvel, 1943. India: Pondichéry, coll. M. Maindron, MNHN syntype: A – setiger 2 parapodium, anterior view; B – setiger 10 parapodium, anterior view; C – setiger 25 parapodium, anterior view; D – setiger 40 parapodium, anterior view; E – heterogomph falciger, dorsal neuropodial fascicle, setiger 10; F – heterogomph falciger, ventral neuropodial fascicle, setiger 10; G – heterogomph falciger, ventral neuropodial fascicle, setiger 45.

by setiger 21, reducing further to less than half length of ventral lobe on about setigers 25-35 and absent on posteriormost setigers. No indication of developing epitoky.

Notosetae present from setiger 3, all homogomph spinigers. Neurosetae homogomph spinigers and heterogomph falcigers in dorsal fascicle, heterogomph spinigers and heterogomph falcigers in ventral fascicle. Neuropodial heterogomph spinigers apparently present throughout (many anterior setae broken).

Remarks. The locality and collector of the specimen examined agrees with that in the original description and it appears certain that this is one of the five specimens examined by Fauvel (1943); we treat it as a syntype. The specimen agrees well with the original description of Fauvel (1943).

The arrangement of paragnaths on *Perinereis maindroni* is unremarkable for the genus, though they are minute and difficult to discern. However, the shape of the notopodia, with three equal lobes anteriorly and a narrow, elongate dorsal lobe in the middle region, is unique among species of *Perinereis*. The division of the body into three marked regions suggests that the specimens may be all epitokes or subepitokes (contrary to Fauvel [1953: 204] who considered some to be atokous).

Distribution. Known only from Pondicherry, 11°57'N 79°48'E, south-eastern India.

Perinereis majungaensis Fauvel, 1921

Perinereis nuntia var. *majungaensis* Fauvel, 1921: 11-13.

Material examined. Madagascar ["Majunga"], MNHN A431, 1 specimen.

Description. A single specimen incomplete posteriorly, size not recorded, gravid female. Paragnaths (given as left, right for paired Areas): I = 8; II = 19, 21; III = about 40 in 3-4 rows; IV = 23, 21 cones, and 13, 12 bars; V = 0? (damaged); VI = 10, 10 bars; VII-VIII = 57 large cones in 2 rows.

Remarks. We do not know if the single specimen we have been able to examine was part of Fauvel's original material of *P. nuntia majungaensis*, which comprised nine specimens. Fauvel's (1921) description provides the following additional information: I = 7-13; II = 20-30; III = 40-50 in four rows; V = 1; VI = 8-10; VII-VIII = three rows of cones. (We have described the specimen examined in this study as having only two rows of cones on Area VII-VIII, but since these cones are irregularly arranged these rows are difficult to describe precisely and little weight can be given to this possible difference.) On the basis of these descriptions, *P. majungaensis* is clearly a distinct species. The high paragnath counts for Areas I, III and the large number of bars on IV distinguish this species from all other species in the *Perinereis nuntia* species-group.

Distribution. Madagascar.

Perinereis matthaii Aziz, 1938

Perinereis matthai Aziz, 1938: 29, pl.3 fig.1, pl.4 figs 29-30, pl.7 figs 56-57.

Description (taken from Aziz, 1938). Prostomium indented anteriorly and with a distinct dorsal groove. Tentacular cirri extend back to setiger 9. Paragnaths: I = 0; II = 4-7; III = cluster of minute, indistinct paragnaths; IV = a cluster; V=0; VI = 6-10 in a transverse row; VII-VIII = absent. Anterior notopodia with 2 unequal lobes. Homogomph spinigers in notopodia, homogomph spinigers and heterogomph falcigers in neuropodia.

Remarks. The absence of paragnaths on VII-VIII distinguishes *P. matthaii* from all other species treated here.

Distribution. Known only from Karachi, Pakistan.

Perinereis mictodonta (Marenzeller, 1879)

Nereis mictodonta Marenzeller, 1879: 118-119, pl.2 fig.2.– Izuka, 1912: 148-151, pl.16 figs 1-6.

Description (taken from Marenzeller, 1879). Tentacular cirri extend back 7-8 setigers. Paragnaths: I = 3; II = oblique tapering group; III = a central group with isolated lateral groups; IV = triangular group; V = 3; VI = a single row of heterogeneous bars; VII-VIII = 3 rows of large cones. Notopodia and neuropodia each with 2 lobes throughout, dorsal notopodial lobe not strongly expanded on posterior setigers.

Remarks. *Nereis mictodonta* was synonymised with *Perinereis nuntia brevicirris* (Grube, 1857) by Imajima (1972), with the following paragnath counts: I = 2-5; II = 22-26; III = about 40; IV = 40-43; V = 3; VI = 4-10 cones and bars; VII-VIII = 34-38 cones in three irregular rows. These counts would exclude this species from *P. nuntia* as diagnosed here (see values in Table 4), however, Imajima also records *P. nuntia vallata* (Grube, 1857) from Japan, with similar but slightly lower paragnath counts. Both taxa described by Imajima (1972) appear very similar to *Perinereis nuntia* (Savigny, 1818) but since we have been unable to examine any material from Japan we defer judgement on the identity of *P. mictodonta*.

Distribution. Japan.

Perinereis namibia n.sp.

Fig.10a-k

Perinereis nuntia vallata.–Day, 1967: 334, fig.14.12.p-s (in part, material from South Africa; not Grube, 1857).

Type material examined. HOLOTYPE: South Africa: Griffiths Bay, Lüderitz, Stn C, coll. S. Penrith & B. Kensley, Mar. 1968, SAMC A20263. PARATYPES: type locality, SAMC A21421, 25 paratypes; type locality, NMV F52582-52584, 3 paratypes; Griffiths Bay, Lüderitz, coll. S. Penrith & B. Kensley, 19 Mar. 1968, SAMC A20078, 4 paratypes.

Additional material examined. South Africa: Lüderitz Bay, coll. L. Schultze, July 1903, ZMB 45109b, 7 specimens. Walvis Bay, Stn WBIF, coll. C. Berrisford, 24 Sept. 1964, SAMC A20030, 2 specimens.

Description (based on type series). Thirty-four

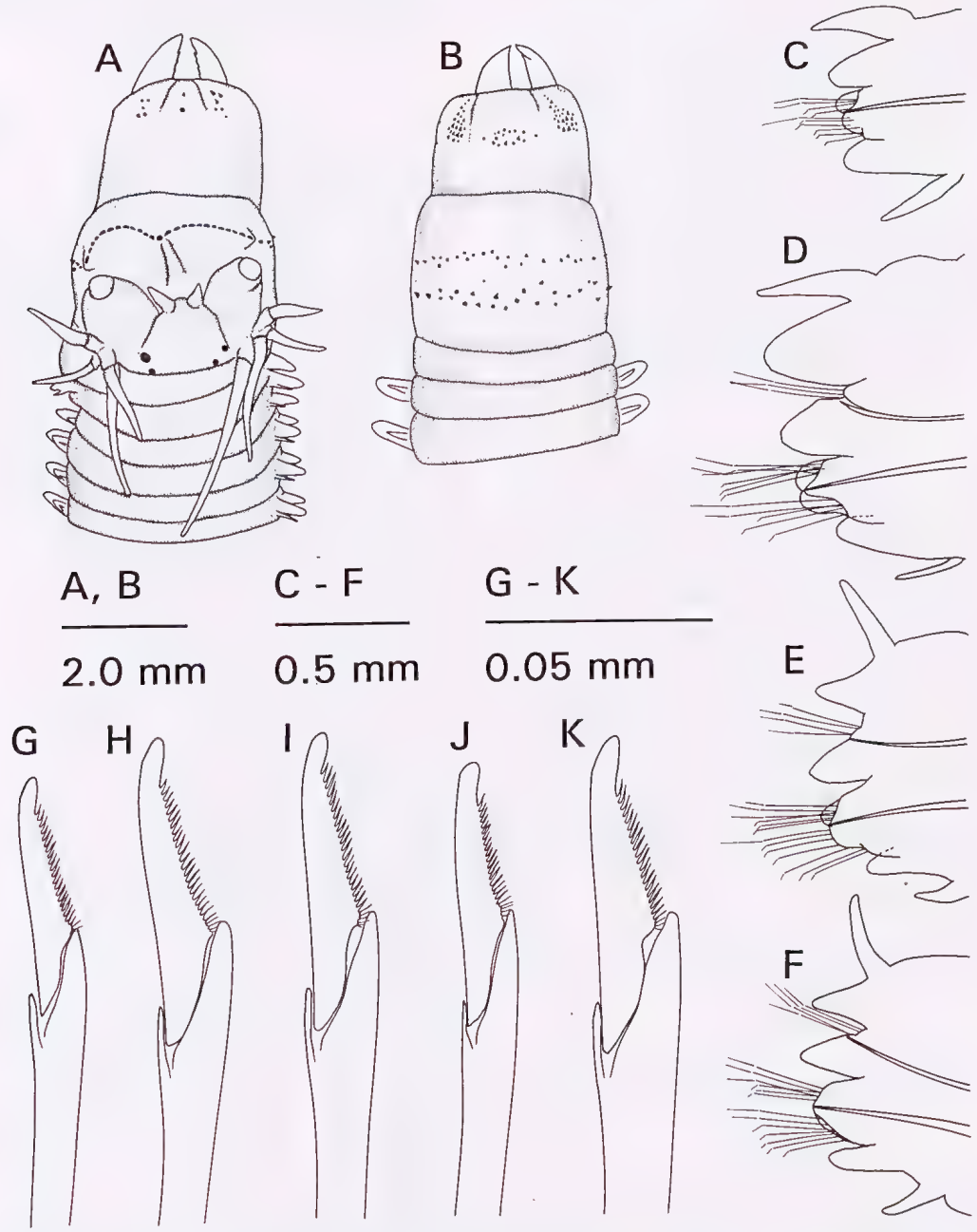

Fig.10. *Perinereis namibia* n.sp. South Africa: Griffiths Bay, Lüderitz, Stn C, coll. S. Penrith & B. Kensley, 19 Mar. 1968, NMV F52582, paratype: A – extended proboscis, dorsal view; B – extended proboscis, ventral view; C – setiger 1 parapodium, anterior view; D – setiger 11 parapodium, anterior view; E – setiger 50 parapodium, anterior view; F – setiger 78 parapodium, anterior view; G – heterogomph falciger, ventral neuropodial fascicle, setiger 1; H – heterogomph falciger, ventral neuropodial fascicle, setiger 11; I – heterogomph falciger, ventral neuropodial fascicle, setiger 78; J – heterogomph falciger, dorsal neuropodial fascicle, setiger 1; K – heterogomph falciger, dorsal neuropodial fascicle, setiger 78.

specimens, 31 setigers (incomplete posteriorly), length 10 mm, width 0.8 mm, jaw length 0.8 mm to 63 setigers (incomplete posteriorly), length 72 mm, width 7 mm, jaw length 3.7 mm. Brown pigmentation on anterior dorsum. Eyes black. Length of prostomium equal to width. Antennae one-third to half as long as prostomium. Tentacular cirri extend back 3-6 setigers. Jaws dark brown, with 4-6 teeth. Paragnaths: I = 1-4; II = 1-20; III = 11-26 (distinct lateral groups present); IV = 5-39 cones, bars absent; V = 0-3; VI = 5-14 bars; VII-VIII = 43-73 large cones in 2-3 rows. Anal cirri as long as posteriormost 5 setigers.

Notopodia with 2 triangular lobes, of similar length and unchanged proportions on posterior setigers. Digitiform presetal notopodial lobe present from setigers 5-25. Dorsal cirri basally inserted, equal in length to notopodial lobes anteriorly, slightly longer than notopodial lobes from about setiger 50. Neuropodia anteriorly with 2 rounded lobes of similar length, dorsal lobe bifid. Ventral neuropodial lobe becoming more acute and shorter than dorsal lobe from about setiger 10. Dorsal neuropodial lobe not noticeably bifid posterior to about setiger 50. Ventral cirri equal in length to neuropodial lobes anteriorly, becoming relatively shorter from about setigers 10-20. Neuropodial heterogomph spinigers present throughout.

Remarks. Descriptive statistics for paragnath counts are provided in Table 4. Two specimens from Walvis Bay (SAMC A20030) possess two to three small bars on Area IV, and appear similar to *Perinereis vallata*. However, these are the only two among 43 specimens with any indication of bar-shaped paragnaths on IV. None of many hundreds of specimens of *Perinereis vallata* examined lacked bar-shaped paragnaths on IV and we prefer to identify these distinctive specimens from southern Africa as a new species: *P. namibia*. *Perinereis vallata* has not been collected in southern Africa.

Etymology. The specific name *namibia* is derived from the African country of the same name and is to be treated as indeclinable.

Distribution. Recorded from Walvis Bay and Griffiths Bay on the coast of Namibia.

Perinereis nuntia (Savigny, 1818)

Fig.11a-g

Lycoris nuntia Savigny, 1818: 313.–Savigny, 1820: 33, pl.4 fig.2.

Neanthes nuntia.–Gravier, 1899: 237 (Savigny, 1818 record repeated).–Fauvel, 1911: 382-383 (Bouchir [=Bushehr], Persian Gulf).

Perinereis nuntia "typique".–Fauvel, 1919: 415 (Djibouti, Gulf of Aden).

Perinereis heterodonta Gravier, 1901: 179, figs 179-181, pl.11 fig.46.–Fauvel, 1911: 394-395.

Perinereis nuntia var. *heterodonta*.–Fauvel, 1919: 419-420 (Djibouti, Gulf of Aden).

Perinereis nuntia var. *djiboutiensis* Fauvel, 1919: 420-421 (Djibouti, Gulf of Aden).

Nereis (Perinereis) heterodonta var. *mictodontoides* Augener, 1913: 177-178.

Nereis (Perinereis) rumphii Horst, 1919: 60.–Horst, 1924: 166-168, pl.33 figs 1-3.

Perinereis broomensis Hartmann-Schröder, 1979: 117-118, figs 211-215.–Hartmann-Schröder, 1980: 60 (new synonymy).

Perinereis weijhouensis Wu *et al.*, 1981: 181-183, figs 114a-k, 115a-d.–Wu *et al.*, 1985: 201-204, figs 114a-k, 115a-d.

Nereis (Lycoris) quatrefagesi Grube, 1878: 79-80.

Perinereis quatrefagesi.–Hylleberg *et al.*, 1986: 5-8, figs 3a-l, 4a-j.

Material examined. RED SEA: coll. de Joussaume, 1894, MNHN jar A108, 9 specimens examined of a total of 15 labelled *Neanthes (Lycoris) nuntia*.

GULF OF ADEN: Djibouti, Illes Musha, à mer basse, dans les fentes des rochers de l'île Maskali, 23 Jan. 1904, MNHN, 8 specimens (material of Fauvel, 1919, but not identified); Djibouti, dans le sable vaseux à l'est de la Résidence, 2 Feb. 1904, MNHN jar A97, 4 syntypes *Perinereis nuntia* var. *djiboutiensis*; Djibouti, Gravier collection, sud du plateau du Serpent, MNHN jar A97, 1 syntype *Perinereis nuntia* var. *djiboutiensis*; Djibouti, Feb. 1933, MNHN jar A97, 9 specimens; Djibouti, 23 Feb. 1904, MNHN jar A97, male epitoke labelled *Perinereis nuntia* var. *heterodonta*; Djibouti, Gravier collection, MNHN jar A526, 4 syntypes *Perinereis heterodonta*; Djibouti, Obock, coll. de Joussaume, 1895, MNHN jar A98 (7 specimens, labelled paratypes; here considered to be syntypes of *Perinereis heterodonta*); Djibouti, Obock, 11 Mar. 1933, MNHN, 6 specimens.

THAILAND: Rawai Beach, Phuket Island, sandy beach, coll. A. Nateewathana, 24 Mar. 1986, PMBC, 5 specimens labelled *P. quatrefagesi*.

PHILIPPINES: Bohol, coll. Semper, WMP 320, 1 syntype *Nereis (Lycoris) quatrefagesi*.

MALAYSIA: Batu Muang, mangrove, coll. Leong Tak Seng, no date, AM W21387, 12 specimens.

INDONESIA: off south coast of East Flores, coll. van der Sande, 14 Jan. 1909, ZMA V.Pol 911, 1 syntype *P. rumphii*.

CHINA: Guangxi, Weijhou, intertidal rock, 16 Apr. 1978, material loaned by Sun Ruiping, 4 specimens identified as *P. weijhouensis*; Zhejiang Province, coll. Zhang Song Ling, 13 Apr. 1984, AM W199677, 1 specimen.

HONG KONG: Starfish Bay (south), upper shore under stones, coll. A.S.Y. Mackie, 5 Apr. 1986, NMWZ 1986.079.142-143, 5 specimens; Starfish Bay (south), low tide from rocks & oysters, coll. A.S.Y. Mackie, 3 Apr. 1986, NMWZ 1986.079.144, 1 specimen; east side of Ping Chau, intertidal in gravel, coll. A. Hirayama, 15 Apr. 1986, NMWZ 1986.079.145, 1 specimen; Tsim Bei Tsui, high tide in mud under stones, coll. R. Gibson, 10 Apr. 1986, NMWZ 1986.079.146, 1 specimen; Tso Wo Hang, below mangroves, mud-shell-sand, coll. P.G. Oliver, 6 Apr. 1986, NMWZ 1986.079.147, 2 specimens.

AUSTRALIA: WESTERN AUSTRALIA: Shark Bay, Denham, Stn 65, ZMB 5275, 1 syntype *Perinereis heterodonta* var. *mictodontoides*; Denham, coll. Michaelsen & Hartmeyer, HZM V7922, 2 syntypes *Perinereis heterodonta* var. *mictodontoides*; Broome, Crab Creek, mangroves, coll. G. Hartmann-Schröder, 11 Sept. 1975, HZM P15520, 2 paratypes *Perinereis broomensis*; Broome, main wharf, intertidal under rocks, coll. R. Hanley, 2 Oct. 1984, NTM W2305, 1 specimen;

Enderby Island, mangroves, intertidal, coll. P.A. Hutchings, AM W201967-8, 3 specimens. NORTHERN TERRITORY: Danger Point, Port Bremer, intertidal, under rocks, coll. R. Hanley, 30 May, 1982, NTM W215, 17 specimens. QUEENSLAND: Yorkeys Knob, intertidal, under rocks, coll. R. Hanley, 19-20 Nov. 1984, NTM W2364, W2365, 3 specimens; Proserpine, coll. A. Hansen, Mar. 1973, QM G10508, 1 specimen; Sandgate, coll. R. Hamlyn-Harris, QM G10497, 4 specimens; Dunwich, Stradbroke Island, intertidal mud flats, coll. University of Queensland, 1 Aug. 1956, QM G4014, 1 male epitoke & 2 atokes; Dunwich, Stradbroke Island, sand and mud, coll. H. Krause, 18 Mar. 1961, QM G7125, 1 specimen.

FIJI: Ngoloa Island, beach on south-east shore, coll. C.J. Glasby, 18-19 Feb. 1987, NMV F53984, 16 specimens.

Description (based on 9 specimens from Red Sea, MNHN A108). Nine specimens, 104 setigers (entire worm), length 48 mm, width 1.8(3.0) mm, jaw length 1.7 mm to 78 setigers (incomplete posteriorly), length 67 mm, width 4.5 mm, jaw length 3.0 mm. Pigmentation absent. Eyes red-black with opaque lenses. Prostomium half as long as wide. Antennae three-quarters as long as prostomium. Tentacular cirri extend back 6-14 setigers. Jaws dark brown, with 5-6 teeth. Paragnaths: I = 1-3; II = 5-9; III = 9-17 (distinct lateral groups present); IV = 9-18 cones, bars absent; V = 0-4; VI = 6-9 bars and cones; VII-VIII = 18-38 large cones in 1-2 rows. Anal cirri as long as posteriormost 11 setigers. Neuropodial heterogomph spinigers present throughout.

Syntypes of *Perinereis heterodonta* var. *mictodontoides* comprise 3 specimens, 175 setigers (entire), length 105 mm, width 1.8(2.8) mm, jaw length 1.6 mm to 208 setigers (entire), length 140 mm, width 3.5(4.5) mm, jaw length 2.6 mm. Pigmentation absent. Eyes black. Length of prostomium equal to width. Antennae half as long as prostomium. Tentacular cirri extend back 3-8 setigers. Jaws dark brown, with 6 teeth. Paragnaths: I = 1-2; II = 1-8; III = 8-14 (distinct lateral groups present); IV = 10-25 cones, bars absent; V = 3-4; VI = 8-13 bars; VII-VIII = 25-31 large cones in 2 rows. Anal cirri as long as posteriormost 6 setigers.

Syntype of *Nereis (Lycoris) quatrefagesi* in very poor condition, comprising 2 anterior fragments for a total of 72 setigers. Body appears almost completely digested, only pale empty skin remaining. Paragnaths in all Areas

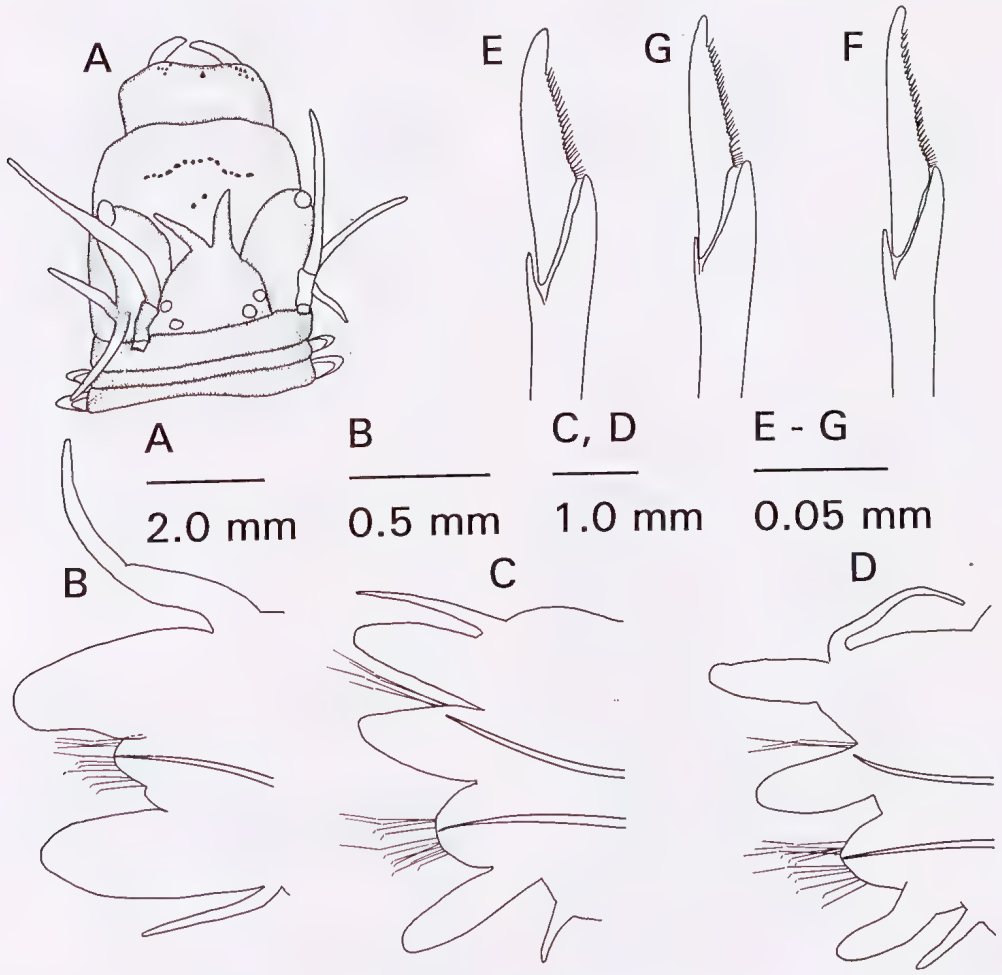

Fig.11. *Perinereis nuntia* (Savigny, 1818). Coll. Jousseaume, 1898, MNHN jar A108: A – extended proboscis, dorsal view; Mer Rouge, coll. Jousseaume, 1894, MNHN jar A108: B – setiger 1 parapodium, anterior view; C – setiger 40 parapodium, anterior view; D – setiger 76 parapodium, anterior view; E – heterogomph falciger, ventral neuropodial fascicle, setiger 3; F – heterogomph falciger, ventral neuropodial fascicle, setiger 40; G – heterogomph falciger, ventral neuropodial fascicle, setiger 76.

have become transparent but can still be counted and general form of soft parts including parapodia are visible. Many setae remain and although all setal types are identifiable, few are intact. Paragnaths: I = 3 (in longitudinal series); II = 7,8; III = 11 (distinct lateral groups present); IV = 16, 18 cones, bars absent; V = 1; VI = 7,8 evenly sized short bars; VII-VIII = 18 in 1-2 uneven rows.

Syntype of *Perinereis rumphii* a mature female epitoke of 159 setigers, jaw length 2.3 mm. Pigmentation absent. Eyes enlarged, red-black. Neuropodial heterogomph spinigers absent. Epitokous parapodia from setiger 30. Dorsal cirri inflated basally setigers 1-6, ventral cirri inflated on setigers 1-4. Dorsal cirri 2 times length of notopodia on setigers 1-6, similar in length to notopodia on median setigers, 3-4 times length of notopodia on posterior 20-30 setigers.

Paragnath count statistics for all material examined are provided in Table 4. Neuropodial heterogomph spinigers absent from anteriormost 3-80 setigers in some specimens.

Remarks. The material listed above is identified as *P. nuntia* (Savigny, 1818) on the basis of the subsequent records of Gravier and Fauvel cited in the synonymy above. Savigny's original material probably no longer exists, however examination of 49 specimens from the vicinity of the type locality indicates that only one species is present in the region and there is little doubt that the name *Perinereis nuntia* is correctly applied to this material.

Perinereis nuntia and several varieties named by Fauvel (1932) have been reported from throughout the southern oceans, South-east Asia, China and Japan. We have referred many of these records to other species of *Perinereis* in this paper; the remaining records will require critical re-appraisal.

Perinereis nuntia appears to exhibit regional variation. Material from the Red Sea has generally lower paragnath values, especially for Areas I, IV, V and VII-VIII, than material from the Indo-Pacific (Fig.3). A possible exception to this pattern is the animals figured by Savigny (1820: pl.4 figs 2.3, 2.4), which have the following paragnath counts: I = 1; II = 9, 7; III = 15; IV = 14, 15; V = 5; VI = 11, 9; VII-VIII = 41. Savigny's figures imply higher paragnath counts than those from any other Red Sea specimens that we have examined, but they may not be accurate. Some separation of populations from these regions in the canonical variates analysis is evident. As discussed in the Statistical Analysis section (above), this separation of the material is not sufficient to justify recognising western and eastern species among the material here referred to *P. nuntia*. The contrary pattern of variation suggested by Savigny's figures also does not support the recognition of two species.

Distribution. Red Sea, Gulf of Aden, and widely distributed throughout the tropical Indo-Pacific, from Thailand, China and Hong Kong, to Australia (north of 27°S), and Fiji.

Perinereis ponuiensis Augener, 1927

Nereis (Perinereis) ponuiensis Augener, 1927: 349-352, figs 5-6.

Material examined. New Zealand: Ponui Island, Auckland, coll. Mortensen, HZM V9725, 1 SYNTYPE; Rangitoto Island, Auckland Harbour, 27 Dec. 1914, ZMK, 1 SYNTYPE.

Description. Two specimens, 50 setigers (incomplete posteriorly), length 48 mm, width 3.5(5.2) mm, jaw length 2.2 mm to 103 setigers (entire), length 85 mm, width 3.0(4.5) mm, jaw length 3.5 mm. Brown pigmentation on anterior dorsum. Eyes black. Length of prostomium half to 1 times width. Antennae half to three-quarters as long as prostomium. Tentacular cirri extend back 5-8 setigers. Jaws dark brown, with 4-5 teeth. Paragnaths: I = 1-2; II = 5-10; III = 8-9 (distinct lateral groups present); IV = 12-25 cones, bars absent; V = 1-2; VI = 4 bars; VII-VIII = 26-27 large cones in 1-2 rows. Anal cirri as long as posteriormost 4 setigers. Superior notopodial lobe 1.5-2 times length of inferior notopodial lobe from about setiger 50. Neuropodial heterogomph spinigers present throughout.

Remarks. Paragnath counts for *Perinereis ponuiensis* are within the range of variation seen in *P. nuntia*. We have retained *P. ponuiensis* as a distinct species on the basis of the apparent constancy of paragnath counts for Area VI: all four specimens described by Augener (1927) possessed only three or four paragnaths on each side in Area VI. The corresponding paragnath counts for *P. nuntia* examined in this study (83 specimens) range from four to 13 with a mean of about seven. The elongation of the superior notopodial lobe on posterior setigers also distinguishes *P. ponuiensis* from *P. nuntia*.

Distribution. Known only from the type material, from Auckland Harbour, North Island, New Zealand.

Perinereis rhombodonta Wu, Sun & Yang, 1981

Perinereis rhombodonta Wu, Sun & Yang, 1981: 179-181, fig.113a-j.–Wu, Sun & Yang, 1985: 199-201, fig.113.

Material examined. CHINA: Guandong, intertidal, sand, coll. Sun Ruiping, 26 May 1976, SRP, 3 specimens; Guangxi, intertidal sand, coll. Sun Ruiping, 20 May 1976, SRP, 3 specimens.

HONG KONG: Starfish Bay (north), mud to high intertidal gravel, coll. C. Erséus, 4 Apr. 1986, NMWZ 1986.079.148, 5 specimens; Starfish Bay (north), shore, coll. R. Gibson, 12 Apr. 1986, NMWZ 1986.079.149, 1 specimen; Starfish Bay (south), high intertidal, sand-mud-clay, coll. A.S.Y. Mackie, 5 Apr. 1986, NMWZ 1986.079.150-151, 11 specimens; Tso Wo Hang, just below mangroves, mud-shell-sand, coll. P.G. Oliver, 6 Apr. 1986, NMWZ 1986.079.152-153, 10 specimens.

THAILAND: Prachuabkirihan Province, Red Shore village, small rocks on beach, coll. Nateewathana & Hylleberg, 10 July 1982, PMBC, 4 specimens.

Description (based on material from China). Size range 61 setigers (regenerating anterior fragment), 19 mm long, 1.2(1.6) mm wide, to 107 setigers (entire), 52 mm long, 1.6(2.6) mm long (jaw length not recorded). No distinctive pigmentation. Eyes black. Prostomium half as long as wide. Antennae one-third to one-quarter as long as prostomium. Longest tentacular cirri extend back 10-11 setigers. Jaws translucent brown , with very small teeth. Paragnaths: I = 2-6; II = 29-64; III = 40-150 in 3-4 groups of similar size; IV = 45-131 cones, bars absent; V = 1-3; VI = 9-14 bars; VII-VIII = 40-59 large cones in 1-2 rows, and 81-110 very small cones arranged in 5-6 similar-sized rhomboidal groups anterior to the large cones. Anal cirri as long as posterior-most 8-10 setigers.

Notopodia with 2 similar conical lobes from setiger 2, and basally inserted dorsal cirri of equal length. Digitiform presetal notopodial lobe absent. Neuropodia with 2 lobes, dorsal lobe more rounded and shorter throughout, ventral lobe more acute and similar in shape and length to notopodial lobes. Ventral cirri about three-quarters length of ventral neuropodial lobe and basally inserted. All parapodial lobes more slender on posterior setigers but proportions otherwise similar throughout. Neuropodial heterogomph spinigers present throughout.

Remarks. The arrangement of paragnaths on Area VII-VIII, with distinctive rhomboidal groups anterior to the larger cones, is unique in the genus *Perinereis*. This species has been adequately figured by Wu *et al.* (1981, 1985).

Distribution. Southern China, newly recorded here from Hong Kong and Thailand.

Perinereis vallata (Grube, 1858)

Fig.12a-l,13a-g

Nereis vallata Grube, 1858: 159-160.
Nereilepas brevicirris Grube, 1867: 19, pl.2 fig.2.
Perinereis vallata.–Hartman, 1954: 35
Perinereis nuntia vallata.–Knox & Cameron, 1971: 28.
Perinereis nuntia.–Hutchings & Turvey, 1982: 139-140.–Hartmann-Schröder, 1984: 29.–Hartmann-Schröder, 1985: 76.–Hartmann-Schröder, 1986: 50.–Hartmann-Schröder, 1987: 48-49 (not Savigny, 1818).
Perinereis sp. B Wilson, 1993: 248, fig.7B.

Material examined. AUSTRALIA: WESTERN AUSTRALIA: Quaramup Jetty, Princess Royal Harbour, south of Albany, WAM 41-87, 1 specimen. SOUTH AUSTRALIA: Spencer Gulf: Corny Point, under rocks, coll. W. Zeidler, 12 Oct. 1974, SAMA E1632, 4 specimens; Blythe Island, intertidal in gravel under rocks, coll. S. Parker, 29 Jan. 1986, SAMA E1633, 7 specimens; Reevesby Island, intertidal in gravelly sand under rocks, coll. S. Parker, 23 Jan. 1985, SAMA E1634, 14 specimens. Gulf St Vincent, outer harbour mudflats and mangroves, coll. L. Duncan, 11 Apr. 1975, SAMA E1635, 1 specimen. Onkaparinga estuary, coll. G. Petersen, 1973, SAMA E1636, 7 specimens. Port Willunga Reef, coll. R.L. Jentz, 22 Sept. 1968, NMV F53997, 8 specimens. VICTORIA: Apollo Bay breakwater, intertidal under rocks, coll. R.S. Wilson, 2 Nov. 1984, NMV F53972, 21 specimens; Separation Creek, intertidal under rocks, coll. R.S. Wilson, 28 Oct. 1985, NMV F53983, 20 specimens; Port Phillip Bay, Werribee, Murtcaim main drain, intertidal in coarse shell, coll. R.S. Wilson, 18 Sept. 1985, NMV F53998, 19 specimens; Western Port, Flinders, south end of Kennon Cove, intertidal under rocks in muddy sand, coll. R.S. Wilson, 3 Sept. 1984, 21 specimens (part of material of Wilson, 1993). TASMANIA: Stanley, Godfrey Beach, on rocks, coll. B.J. Smith, 30 Nov. 1968, NMV F53999, 4 specimens; Bicheno, coll. B.J. Smith, 22 Nov. 1968, NMV F54000, 9 specimens; Coles Bay, intertidal cobble, Stn TAS 13, coll. R.S. Wilson, 21 Apr. 1985, NMV F54001, 2 specimens; Flinders Island, Franklin Sound, coll. Essendon Grammar, 25 Nov. 1922, NMV F54002, 6 specimens; Flinders Island, Petrefaction Bay, under rocks in sandy mud, coll. T. Cochrane, 16 May 1986, NMV F54003, 1 specimen. NEW SOUTH WALES: Quarantine Bay, intertidal in sand under rocks, coll. R.S. Wilson, 17 July 1987, NMV F54005, 2 specimens; Botany Bay, 1910, AM W181, 15 specimens.

MACQUARIE ISLAND: NMV F54004, 1 specimen.

NEW ZEALAND: Auckland, 1924/6? [label unclear], MNHN unregistered, 12 specimens in 2 vials; Wellington, coll. M. Filhol, "No. 28", 1875, MNHN A97, 9 specimens.

ST PAUL ISLAND: coll. A.E. Grube, ZMB Q3463, 1 SYNTYPE *Nereilepas brevicirris*.

CHILE: Valparaiso, coll. Krøyer, ZMK unregistered, 5 SYNTYPES *Nereis vallata*. Ancud, coll. C. Rebolledo, Dec. 1984, NR, 11 specimens.

Description (based on 5 syntypes of *Nereis vallata* Grube, 1858). Size range 54 setigers (anterior fragment), 42 mm long, 2.7(4.1) mm wide to 126 setigers (anterior fragment), 115 mm long, 4.0(6.0) mm long (jaw length not recorded). Pigmentation a single transverse dark band dorsally on each segment on the anterior half of the body. Eyes black. Length of prostomium equal to width. Antennae half as long as prostomium. Tentacular cirri extend back 3-7 setigers. Jaws dark, with no teeth (possibly worn). Paragnaths: I = 2; II = 6-18; III = 18-32 (distinct lateral groups present); IV = 26-40 cones, 0-3 bars (bars absent on one side in one specimen); V = 0-2; VI = 12-16 bars; VII-VIII = 62-89 large cones in 2-3 rows. (Paragnath count statistics for all material examined are provided in Table 4.) Anal cirri as long as posteriormost 4-9 setigers.

Notopodia with 2 triangular lobes, of similar length and unchanged proportions on posterior setigers. Digitiform presetal notopodial lobe present on setigers 5-25. Dorsal cirri basally inserted, equal in length to notopodial lobes anteriorly, slightly longer than notopodial lobes from about setiger 50. Neuropodia anteriorly with 2 rounded lobes of similar length, dorsal lobe bifid. Ventral neuropodial lobe becoming more acute and shorter than dorsal lobe from about setiger 10.

Dorsal neuropodial lobe not noticeably bifid posterior to about setiger 50. Ventral cirri equal in length to neuropodial lobes anteriorly, becoming relatively shorter from about setigers 10-20. Neuropodial heterogomph spinigers present throughout.

Remarks. *Perinereis vallata* is the most common species in the *P. nuntia* species group in southern Australia and Chile, however, similar species also occur in both areas and most published records need to be re-examined. Nevertheless, it is likely that most of the records of *P. nuntia brevicirris* and *P. nuntia vallata* in Day & Hutchings (1979) refer to *Perinereis vallata*. The variability in paragnath counts and parapodial form between *P. vallata* from Australia, New Zealand and Chile is no greater than that observed by Wilson (1993) among populations in south-eastern Australia.

Distribution. Southern Australia from Albany, WA to Botany Bay, NSW, Macquarie Island, New Zealand, St Paul Island and Chile.

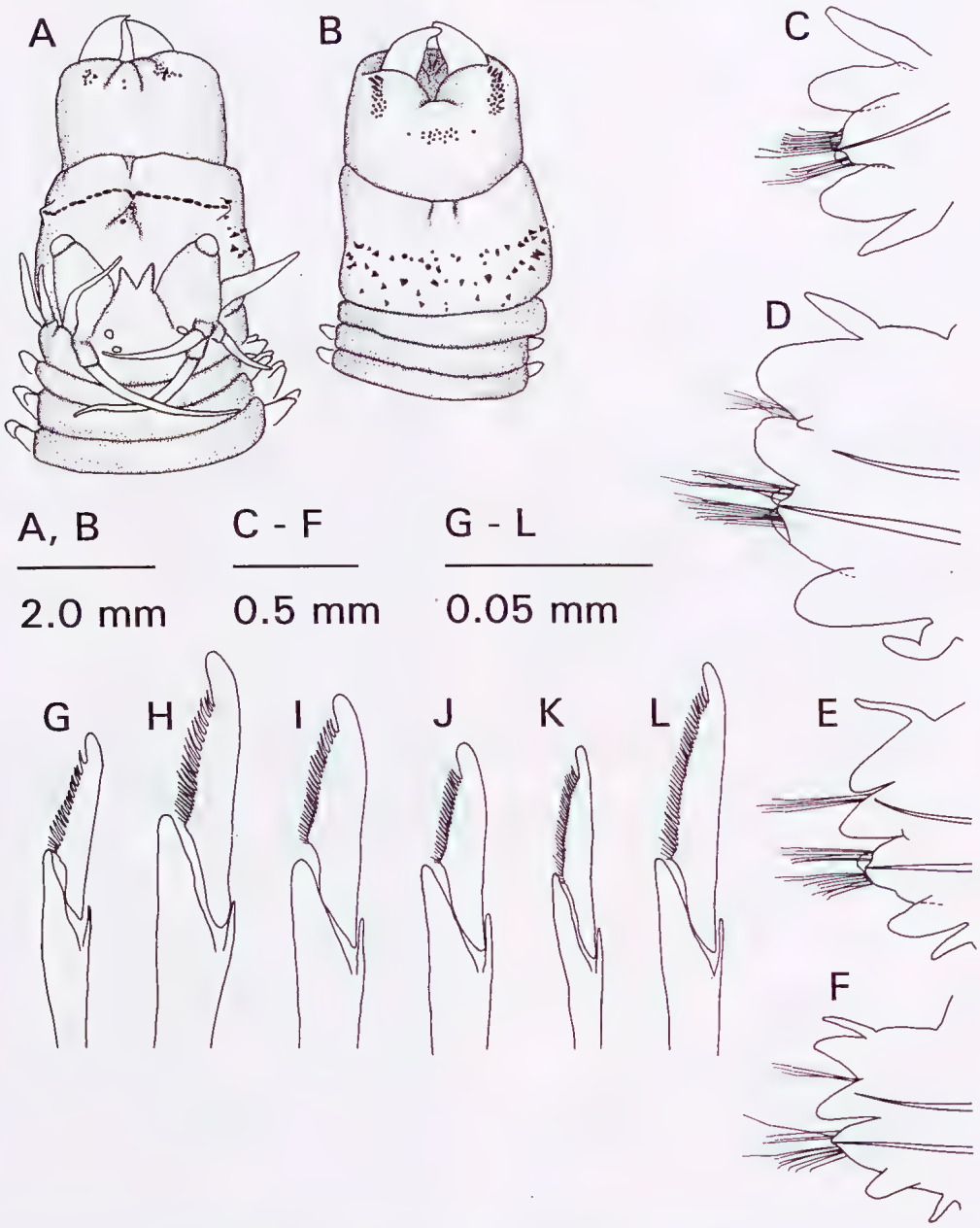

Fig.12. *Perinereis vallata* (Grube, 1857). Victoria, Apollo Bay breakwater, 30 Oct. 1985, NMV F53971: A – extended proboscis, dorsal view; B – extended proboscis, ventral view; C – setiger 1 parapodia, anterior view; D – setiger 10 parapodia, anterior view; E – setiger 50 parapodia, anterior view; F – setiger 110 parapodia, anterior view; G – heterogomph falciger, dorsal neuropodial fascicle, setiger 1; H – heterogomph falciger, dorsal neuropodial fascicle, setiger 10; I – heterogomph falciger, dorsal neuropodial fascicle, setiger 44; J – heterogomph falciger, dorsal neuropodial fascicle, setiger 110; K – heterogomph falciger, ventral neuropodial fascicle, setiger 1; L – heterogomph falciger, ventral neuropodial fascicle, setiger 10.

Perinereis sp. 1 [Juan Fernandez]

Nereis vallata.–Ehlers, 1901: 110-112 (in part, material from Juan Fernandez Islands; not Grube, 1857).

Material examined. Juan Fernandez Islands, coll. Plate, 20 fathoms, ZMB 3728 (material of Ehlers, 1901).

Description. One specimen, 102 setigers (incomplete posteriorly), length not recorded, width 2.6(5.2) mm, jaw length 2.3 mm. Pigmentation absent. Length of prostomium equal to width. Antennae half as long as prostomium. Tentacular cirri extend back 7 setigers. Jaws dark brown, teeth worn. Paragnaths: I = 2; II = 4, 9; III = 24 (distinct lateral groups present); IV = 24, 20 cones, bars absent; V = 2; VI = 11, 14 bars; VII-VIII = 68 large cones in 2-3 rows. Anal cirri lost. Neuropodial heterogomph spinigers present from setiger 3.

Remarks. This specimen is similar to *P. namibia* from South Africa and is within the range of variation for paragnath counts recorded for that species, however we are unwilling to extend the range of *P. namibia* to this disjunct locality on the basis of a single specimen. More material from the Juan Fernandez Islands is required for identification of this species.

Distribution. Juan Fernandez Islands, South Pacific.

Perinereis sp. 2 [Indonesia]

Material examined. INDONESIA: Stn 115, Siboga Expedition, ZMA V.Pol 2352, 1 specimen.

Description. A single specimen in poor condition, 217 setigers (entire), length cannot be determined, width 3.5(5.5) mm, jaw length 3.6 mm. Pigmentation absent. Eyes faded. Length of prostomium equal to width. Antennae one-quarter as long as prostomium. Tentacular cirri extend back 4 setigers. Jaws dark brown, with 6-8 teeth. Paragnaths: I = 2; II = 10, 11; III = 34 (distinct lateral groups present); IV = 32, 33 cones, 3, 2 bars; V = 1; VI = 4, 4 high bars, of uneven length; VII-VIII = 51 large cones in 2 rows. Anal cirri as long as posteriormost 8 setigers. Neuropodial heterogomph spinigers present throughout.

Remarks. This specimen differs from other species of *Perinereis nuntia* in having only four high bars of

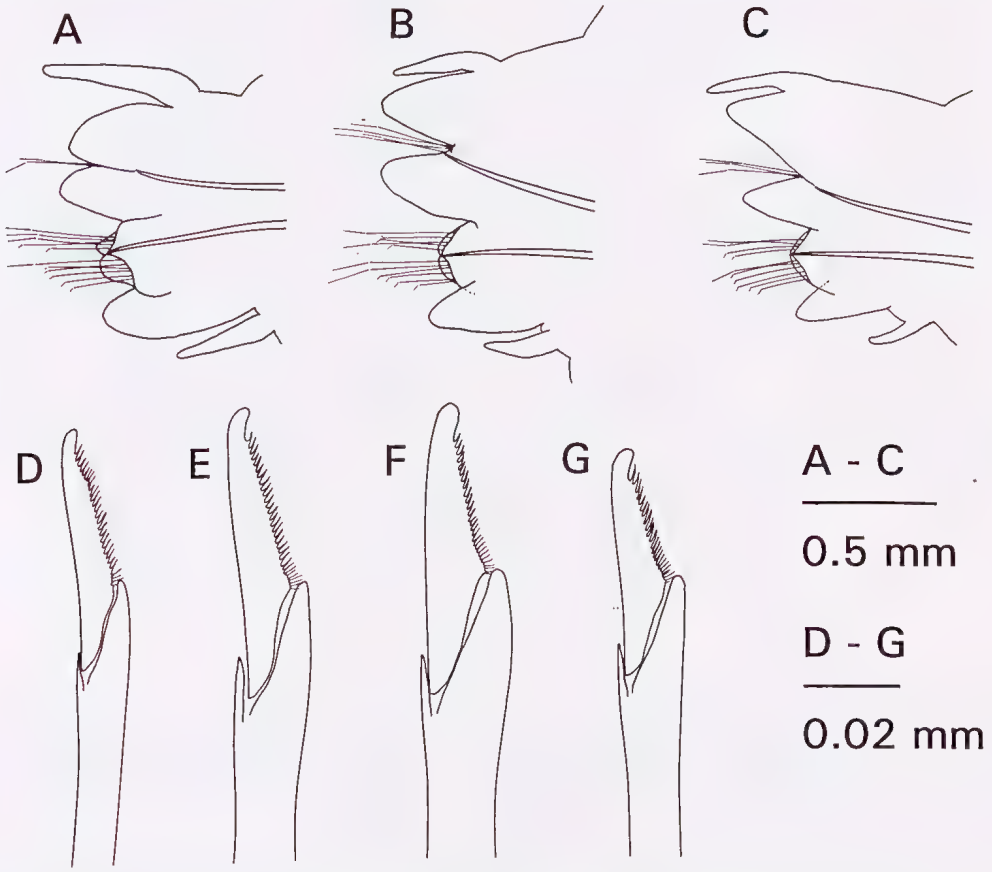

Fig.13. *Perinereis vallata* (Grube, 1857). Chile: Valparaiso, coll. Krøyer, ZMK unregistered, one of five syntypes (142 setiger specimen): A – setiger 3 parapodium, anterior view; B – setiger 40 parapodium, anterior view; C – setiger 130 parapodium, anterior view; D – heterogomph falciger, ventral fascicle, setiger 1; E – heterogomph falciger, ventral fascicle, setiger 40; F – heterogomph falciger, dorsal fascicle, setiger 40; G – heterogomph falciger, ventral fascicle, setiger 130.

uneven length on VI and may represent an undescribed species. However, we prefer not to base a formal description on a single poor specimen. The specimen is labelled *Nereis vallata*, but Horst (1924) did not report that species from the Siboga material. The only *Perinereis* species reported from Stn 115 in Horst's account is *P. singaporiensis*; Horst had four specimens and provided paragnath counts for a single specimen which differ from those for the specimen we have examined. Nevertheless, it is possible that this specimen is part of Horst's original material of *P. singaporiensis*. (*Perinereis singaporiensis* is described in Hutchings *et al.* (1991) and does not belong in the *P. nuntia* complex.)

Distribution. Indonesia.

Discussion

Paragnath shape and number are crucial taxonomic characters in the *Perinereis nuntia* species group. Even poorly preserved or incomplete specimens can usually be identified to species on the basis of paragnath counts, since the retracted proboscis is less likely to be damaged than parapodia and setae. More importantly, intra- and inter-specific variation in paragnath counts is now well understood and most specimens should be identifiable. New qualitative paragnath characters that are taxonomically useful are presence of bars on Area IV, and presence of additional bands of minute paragnaths on Areas VII-VIII.

Previous authors have described taxa partly on the basis of presence of one as against three cones in a triangle in Area V. However, virtually all species may possess one to three paragnaths on Area V, and this arrangement is taxonomically uninformative. The only exception is *Perinereis rhombodonta*, in which Area V always has one paragnath.

Length of the longest pair of tentacular cirri is routinely provided in descriptions but varies considerably within populations. Length of tentacular cirri is usually measured by the number of setigers over which the longest cirrus extends. Since the contraction of the body segments of the worm and of the tentacular cirri are dependent in part on preservation technique, cirrus length is only taxonomically useful where species differ markedly in this characteristic. Among the species described here, most have longest tentacular cirri in the range three to eight setigers long, with only *P. nuntia* (tentacular cirri 6-14 setigers) and *P. rhombodonta* (tentacular cirri 10-11 setigers) being distinct in this respect.

The form of the jaws and their serration are poor taxonomic characters in most species. The jaws are frequently worn to the extent that any serration on the cutting edge is lost. *Perinereis akuna*, *P. maindroni* and *P. rhombodonta*, however, have relatively thin translucent jaws. In all other species the jaws are thick and opaque.

In many genera of nereidids (eg, *Neanthes*) the shape of the parapodia, and the number of parapodial lobes are useful taxonomic characters (Wilson, 1984). Among those species of *Perinereis* treated elsewhere by Hutchings *et al.* (1991) some are readily distinguished by greatly elongated dorsal parapodial lobes of posterior segments. Parapodia in the *Perinereis nuntia* species group, however, are relatively uniform. *Perinereis caeruleis* has expanded (though not elongate) dorsal notopodial lobes on posterior setigers. *Perinereis maindroni* is unique in having three notopodial lobes, with the dorsal lobe narrow and prolonged on median setigers. All other species figured here have very similar parapodia. Ben-Eliahu (1987) suggested an approach to morphometric descriptions of nereidid parapodia. Although a quantitative method for analysis of parapodial form may provide useful data, we lacked facilities to automate Ben-Eliahu's laborious method and relied instead on traditional qualitative comparisons.

Setae, especially falcigers, are usually figured in descriptions of species of *Perinereis*, even though these structures are rarely useful in distinguishing species. Among the species described here, only *Perinereis caeruleis* has distinctive falcigers. The form of the falcigers varies little along the body in *Perinereis nuntia* group species, although falcigers from dorsal fascicles usually have slightly broader blades than those from ventral fascicles.

Artificial Key to Species of the *Perinereis nuntia* Group

This key excludes two species for which we were unable to examine material and which are insufficiently characterised by existing published descriptions: *Perinereis gualpensis* Jeldes, 1963, *P. mictodonta* (Marenzeller, 1879). *Perinereis* sp. 1 [Juan Fernandez] and *Perinereis* sp. 2 [Indonesia], each of which were represented in this study by a single specimen, appear in the key with species from which they cannot presently be differentiated.

1. Anterior 20 notopodia with 3 lobes of similar size ..... *P. maindroni*

—— All notopodia with 2 lobes 2

2. Paragnaths absent from Area II and usually from Area I; an additional arc of cones posterior to the arc of bars on Area VI ..... *P. caeruleis*

—— Paragnaths present on I and II; only a single arc of bars or mixed bars and cones on Area VI 3

3. Paragnaths absent from Area VII-VIII ..... *P. matthaii*

—— Paragnaths present on Area VII-VIII 4

4. Area IV with 3 or more smooth parallel bar-shaped paragnaths in addition to cones 5

—— Area IV with cones only 7

5. Areas VII-VIII with a band of normal conical paragnaths and a distinct posterior band of minute conical paragnaths ..... *P. akuna*

—— Areas VII-VIII without an additional posterior band of minute paragnaths 6

6. Area IV with more than 10 smooth parallel bars; Area III with about 40 cones ..... *P. majungaensis*

—— Area IV with 5 smooth bars at most; Area III with fewer than 35 cones ..... *P. vallata* (& *Perinereis* sp. 2 [Indonesia])

7. Areas VII-VIII with a band of normal conical paragnaths and a distinct anterior band of minute conical paragnaths ..... *P. rhombodonta*

—— Areas VII-VIII without an additional anterior band of minute paragnaths 8

8. Area VI with 3-4 bar-shaped paragnaths ..... *P. ponuiensis*

—— Area VI with 4-17 bar-shaped paragnaths (usually 6 or more) 9

9. Area VII-VIII with 43-76 paragnaths; heterogomph spinigers present in the neuropodia of all setigers ..... *P. namibia* (& *Perinereis* sp. 1 [Juan Fernandez])

—— Area VII-VIII with 10-40 paragnaths (rarely up to 50); heterogomph spinigers frequently absent from a variable number of anterior setigers ..... *P. nuntia*

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APPENDIX

Table 1. Available names, *Perinereis nuntia* species group.

Original combination	Author, year	Type locality
Nereis (Perinereis) binongkae	Horst, 1924	Indonesia
Nereilepas brevicirris	Grube, 1867	St Paul Island
Perinereis broomensis	Hartmann-Schröder, 1979	Western Australia
Heteronereis caeruleis	Hoagland, 1920	Philipines
Perinereis nuntia djiboutiensis	Fauvel, 1919	Gulf of Aden
Perinereis gualpensis	Jeldes, 1963	Chile
Perinereis heterodonta	Gravier, 1899	Red Sea
Perinereis maindroni	Fauvel, 1943	France
Perinereis nuntia majungaensis	Fauvel, 1921	Madagascar
Perinereis matthaii	Aziz, 1938	Karachi, India
Nereis mictodonta	Marenzeller, 1879	Japan
Nereis (Perinereis) heterodonta mictodontoides	Augener, 1913	Western Australia
Perinereis neocaledonica	Pruvot, 1930	New Caledonia
Lycoris nuntia	Savigny, 1818	Gulf of Suez
Nereis (Perinereis) ponuiensis	Augener, 1924	New Zealand
Nereis (Lycoris) quatrefagesi	Grube, 1878	Philipines
Perinereis rhombodonta	Wu Baoling, Sun Ruiping & D.J. Yang, 1985	China
Nereis (Perinereis) rumphii	Horst, 1919	Indonesia
Nereis vallata	Grube, 1857	Chile
Perinereis weijhouensis	Wu Baoling, Sun Ruiping & D.J. Yang, 1985	China

(*Perinereis nuntia bombayensis* Bhatt & Bal, 1966 (described from India) according to the original description, has only conical paragnaths in an arc on Area VI and therefore must be placed in the genus *Neanthes* Kinberg, 1866.)

Table 2. Canonical loadings (correlations between conditional dependent variables and dependent canonical factors), *Perinereis nuntia*-group samples, material lacking bars on Area IV. Factors 1-3 cumulatively account for 92.3% of the total variation.

	Factor(1)	Factor(2)	Factor(3)
I	0.086	0.410	-0.367
IIL	0.119	0.258	0.028
IIR	0.111	0.314	-0.129
III	-0.253	0.234	-0.327
IVLC	-0.247	0.405	-0.350
IVRC	-0.206	0.362	0.085
V	0.352	0.748	0.195
VIL	-0.214	-0.152	-0.198
VIR	-0.214	-0.169	-0.273
VII-VIII	-0.856	0.479	0.074

Table 3. Canonical loadings (correlations between conditional dependent variables and dependent canonical factors), *Perinereis nuntia*-group samples, material with bars on Area IV. Factors 1-3 cumulatively account for 98.2% of the total variation.

	Factor(1)	Factor(2)	Factor(3)
I	-0.007	0.106	0.090
IIL	0.342	-0.102	0.076
IIR	0.386	-0.255	0.124
III	-0.583	0.254	0.285
IVLC	-0.419	-0.231	-0.104
IVLB	0.066	0.029	0.098
IVRC	-0.406	-0.159	-0.088
IVRB	0.172	0.017	-0.028
V	0.177	0.673	-0.021
VIL	-0.190	0.308	-0.726
VIR	-0.243	0.154	-0.753
VII-VIII	-0.031	0.302	-0.139

Table 4. Descriptive statistics, paragnath counts, *Perinereis nuntia*-group.

	I	II	III	IVC	IVB	V	VI	VII-VIII
akuna (n = 27)								
mean±sd	2.4±0.8	14.8±3.6	18.4±3.7	24.9±6.4	2.9±0.9	2.6±1.1	7.5±1.1	116.0±30.4
min-max	1-4	6-21	13-27	11-41	1-5	1-4	5-11	76-191
caeruleis (n = 3)*								
mean	0.7	–	150	100	–	43	13	210
min-max	0-2	–	110-185	85-110	–	39-48	12-15	200-250
namibia (n = 43)								
mean±sd	1.7±0.7	5.5±3.0	16.6±4.0	22.7±5.4	–	0.8±0.6	10.4±1.3	56.4±8.0
min-max	0-4	0-20	10-26	5-39	–	0-3	5-14	43-76
nuntia (n = 132)								
mean±sd	1.8±0.8	6.8±3.0	11.5±4.2	16.5±4.6	–	1.9±1.4	8.2±2.5	28.0±6.2
min-max	0-5	0-23	1-30	5-35	–	0-5	4-17	10-52
ponuiensis (n = 2)								
mean±sd	1.5±0.7	7.5±2.8	8.5±0.7	18.3±7.4	–	1.5±0.7	3.7±0.4	26.5±0.7
min-max	1-2	5-10	8-9	12-25	–	1-2	3-4	26-27
rhombodonta (n = 14)								
mean±sd	4.3±1.3	44.9±10.0	93.6±31.4	84.2±23.8	–	1.1±0.5	11.3±1.5	113.4±36.0
min-max	2-6	29-64	40-142	45-131	–	1-3	9-14	55-165
vallata (n = 427)								
mean±sd	1.6±0.7	11.0±2.5	18.7±4.4	28.1±5.7	2.6±0.6	2.3±1.0	12.5±1.5	69.0±13.6
min-max	0-9	1-23	9-35	0-47	0-5	0-5	5-14	42-129

* Specimens of *P. caeruleis* have paragnaths that are too small, closely spaced and numerous to be counted accurately on dissected specimens.

The Aphroditidae (Polychaeta) from Australia, together with a Redescription of the Aphroditidae collected during the Siboga Expedition

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ABSTRACT. The family Aphroditidae is represented in Australian waters and the Indonesian Archipelago by 34 species in five genera, of which seven are new species. Previously described species from Australia are redescribed. The Aphroditidae collected during the Siboga expedition and described by Horst (1916a,b, 1917) are also redescribed and the relationship of this fauna to the Australian fauna discussed. In addition, the characters used to distinguish genera and species within the family and the variations exhibited by these characters are discussed, to facilitate a subsequent phylogenetic study of the group. A key to the genera and species represented in the Indo-Pacific is given.

HUTCHINGS, P.A. & J. MCRAE, 1993. The Aphroditidae (Polychaeta) from Australia, together with a redescription of the Aphroditidae collected during the Siboga Expedition. Records of the Australian Museum 45(3): 279–363.

The family Aphroditidae is poorly known from Australian waters. Day & Hutchings (1979) recorded 12 species in four genera, some of them are known only from their original descriptions, and for one of these species *Aphrodita terraereginae* no additional material has been found during this study. However, this family is well represented in Museum collections in Australia, especially those from deeper waters.

We have therefore undertaken a comprehensive study of the Australian aphroditids. We have examined all the aphroditid material available in Australian state museums and the extensive collections of aphroditids made during the Siboga Expedition and described by Horst (1916a,b, 1917). In this paper we describe 34 species in five genera, of which seven are new species. For species previously described we have provided comprehensive descriptions as the original descriptions are typically very brief.

Apart from the material collected during the Siboga Expedition few other aphroditids have been described from the Indo-Pacific. It is surprising that there is little overlap between the aphroditid fauna of Australian waters, and those recorded from Indonesian waters, as aphroditids are typically deep water species. However it should be stressed that relatively little material was available from northern Australia, where little deep water collecting has been undertaken.

A recent revision of the genus *Palmyra* by Watson Russell (1989) has placed this genus in the family Aphroditidae. It was considered to be a member of the family Chrysopetalidae by Day (1967) and subsequently

Fauchald (1977) referred to it as belonging to the family Palmyridae. While this genus is included in the key, only a brief description of this monospecific genus is given by us, as no additional material was available other than the material recently described by Watson Russell (1989).

It may seem surprising that so many new species are present in Australian waters, but this can be explained by the fact that although aphroditids are typically large and highly conspicuous members of the benthic fauna, they are predominantly deep water species, and the Australian deep water fauna is not well known. Although many of the species have overlapping geographical distributions, we have virtually no information on the habitats in which these species occur although some species have sand or mud entangled amongst their setae indicating perhaps habitat preferences. With increasing collecting, this should be rectified. During this study we examined large amounts of material collected in the Bass Strait by the Museum of Victoria. While we were able to identify much of this fauna to species, some of the smaller individuals (2-3 mm long) could not be reliably identified to species. This was because some of the small individuals lacked particular setal types, and no studies on setal development and other structures, such as palps and tentacles, with increasing size and presumably age, have been carried out on this family. It may be that juvenile aphroditids cannot be identified to species as we believe, setal structure and composition change markedly during the initial stages of development. While some of these small individuals may represent juveniles of adults described from the region, others may represent undescribed species.

In the literature, a considerable variety of terms have been used to describe aphroditid morphology. In Figures 1, 27, 32 and 52 we illustrate a typical member of each genus considered and indicate the terminology which we have followed.

Material and Methods

The following measurements were recorded for animals examined: total body length, maximum body width including setae and segments, and the number of parapodia. This is summarised for each species, in addition the range of total body length is given for each lot examined.

The keys to the family and genera are artificial and do not imply any phylogenetic relationships.

The following abbreviations have been used in the text: LACM-AHF – Allan Hancock Foundation, Los Angeles, California (Polychaete collections now located at the Los Angeles County Museum); AM – Australian Museum, Sydney; BMNH – The Natural History Museum, London; MTQ – Museum of Tropical Queensland, Townsville; NMV – National Museum of Victoria, now Museum of Victoria, Melbourne; NTM – Northern Territory Museum, Darwin; QM – Queensland Museum, Brisbane; SAM – South Australian Museum, Adelaide; USNM – National Museum of Natural History, Smithsonian Institution, Washington, D.C.; WAM – Western Australian Museum, Perth; ZMA – Zoologisch Museum, Amsterdam; ZMB – Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin.

In each species description we give the known distribution of the species, localities marked * are for localities which appear in the literature but we have not examined material from that area to confirm the identifications.

The specific names are based on Aboriginal words in several languages meaning a shield and were found by consulting 'Australian Aboriginal Words and Place Names and their Meanings' by Sydney E. Endacott (1984).

All tables referred to throughout the text are listed in the Appendix.

The Systematics and Characters considered useful in the Family Aphroditidae

The family Aphroditidae has not been subjected to a comprehensive revision since it was erected by Malmgren (1867). Horst (1916a,b, 1917) described one new genus and 21 new species, subsequently Pettibone (1966) partly revised some of the genera and recognised an additional genus. Fauchald (1977) recognised seven genera, one of these *Tricertia* Haswell, 1883 we have synonymised with *Pontogenia* Claparède, 1868. Of the remaining six genera recognised by Fauchald (1977) we have examined representatives of all except for the monospecific genera *Hermionopsis* Seidler, 1923, and *Heteraphrodita* Pettibone, 1966. More recently, Watson Russell (1989) has placed the monospecific genus *Palmyra* Savigny, 1818 in the family Aphroditidae and she gives an expanded family diagnosis to include this genus.

We have had the opportunity in several cases to examine substantial numbers of individuals of particular species within some genera which has enabled us to study the variation of a character with respect to increasing size and presumably age. Listed below are the characters which we believe are useful in aphroditid taxonomy both at the generic and specific level and the various character states exhibited by each character. At this stage we have rarely attempted to polarise the character states. A more detailed study, including a phylogenetic analysis would resolve many problems, but is clearly beyond the scope of this study. We did not attempt to consider the relationships between the genera. Fauchald (1977) placed the family within the superfamily Aphroditacea, the sub order Aphroditiformia all within the order Phyllodocida. Fauchald gives little explanation of the characters used to determine these orders, and certainly at this time no cladistic study was undertaken, although he is currently undertaking such a study (Fauchald personal communication).

Since many members of the family have been described from deep water in other parts of the world, one would anticipate finding many new taxa from Australia, as deep water areas off this continent are poorly known, and this is indeed what we did find.

The family Aphroditidae is primarily represented by deep water species and few species occur intertidally. It is assumed that they produce a pelagic larval stage although palmyrids have large yolky eggs (300-400μm) which suggests a probable non feeding pelagic stage or direct development with limited ability to disperse (Watson Russell, 1989). No details are known for other members of the family, similarly no development studies have been undertaken of the early stages of any species of aphroditid. We examined material 2 to 3 mm in length from the Bass Strait and could not assign these individuals to species. Watson Russell (1989) indicates that juveniles of *A. australis* Baird and *Pontogenia chrysocoma* Baird collected from hard substrates in shallow water lack elytra, elytrophores, dorsal tubercles and notosetal felt, the major notosetal types are relatively large compared with body size and entirely cover the body. This suggests that juvenile aphroditids are not currently identifiable to species, and the following comments apply only to the adult condition. In the following discussion we consider the constancy of characters over the size range of material examined; it should be noted that for some of the species in the four genera *Aphrodita*, *Aphrogenia*, *Laetmonice*, *Pontogenia*, only the holotype of the species was available for examination.

As no material of *Palmyra* was examined, we have not included it in the discussion below and the reader is referred to the recent study of the single species of *Palmyra*, *P. savigny* by Watson Russell (1989).

In cases where some suggestions are made as to the plesiomorphic and apomorphic condition, we have considered that possible outgroups which could be used in a cladistic study would be a family within the suborder Phyllodociformia such as the family Phyllodocidae or a family within the suborder Nereidiformia such as the family Nereididae. Recent revisions of these families have been undertaken by Glasby (1991), Fitzhugh (1987) and Pleijel (1991) which would facilitate such a study.

Characters

General Body Form

1. Numbers of segments. The numbers of body segments, equal to the number of pairs of parapodia, appears relatively constant for a particular species of *Aphrodita*. For example individuals of *A. kulmaris* n.sp. ranging from 1.8 to 10 cm in length have 38 to 46 segments, whereas *A. bamarookis* n.sp. ranging from 3 to 6 cm in length, have 49 to 52 segments. There appears to be two groups of species of *Aphrodita*, those with a relatively low number of segments (32-36) and those with 40+. Similarly in *Laetmonice* the number of segments appears to be relatively constant for a particular species. Some species have a large number such as *L. producta* Grube (41-45) whereas others have as few as 25 *L. batheia* Horst.

In the single species of *Aphrogenia* examined *A. margaritacea* Augener, the number of segments varied from 22 to 32 over a range of body sizes, suggesting that this species grows initially by increasing the number of segments. We assume that once 32 segments is reached, proliferation of body segments cease. We do not know if this pattern is valid, nor if it represents a species or genus specific pattern.

In *Pontogenia* at least for *P. araeoceras* (Haswell) and *P. macleari* (Haswell), small individuals have fewer segments than larger individuals and there is evidence that adults of these two species have varying numbers of segments. The other two species of *Pontogenia* present in the Indo-Pacific were represented by only a single specimen, so no further comments can be made for this genus.

As aphroditids presumably arose from a long multisegmental ancestral form, one could speculate that the reduction in the number of segments is an apomorphic character. Several species studied exhibited considerable ranges in size such as *Aphrodita kulmaris* n.sp. 1.8 to 10 cm, suggesting a long lived species. We suspect that this is true for all aphroditids and that once a certain number of segments have been attained, growth occurs only by expansion of segments.

2. Body shape. Species of *Aphrodita*, *Aphrogenia* and *Pontogenia* all have a similar body shape although some species of *Aphrodita* have an attenuated caudal region, the significance of which is unknown, although the presence or absence of the attenuated caudal region is constant for a species.

In contrast, species of *Laetmonice* vary in their body shape from elongate, oval in shape to cigar-shaped. Whether this can be used as a specific character is doubtful.

The body shape of aphroditids appears not to be a useful generic or specific character and appears to be more of a familial character.

3. Ventral surface. The ventral surface of all the genera examined was papillated with the papillation becoming more pronounced in larger individuals. The value of this character is unknown although perhaps if an index of papillation in terms of structure and density could be established it could be a useful character.

4. Prostomium. *a) Median antenna.* The structure and shape of the median antenna is a useful specific character, and appears to be constant within a species, regardless of size. In *Aphrodita* the antennal shape varies from small knob-shaped, rod-shaped, bulbous, to an elongate antenna equal or greater in length to the prostomium. In some species of *Aphrodita* the median antenna is biarticulate with a basal ceratophore and an

elongate style, but in other species the antenna appears as a simple structure and no separation of ceratophore and style is apparent. There does not appear to be a relationship between shape and presence of articulation, however all species that have a ceratophore tend to have a long style (three-quarters to one and one-quarter length of prostomium). But not all species with a long antenna have an apparent ceratophore.

In all the other genera the median antenna is always a compound structure consisting of a basal ceratophore and a style. The relative lengths of these two structures varies among species.

In *Pontogenia* the ceratophore may be either smooth or finely papillated as in two species present in Australian waters and the shape of the style varies from those with a finely tapered articulate tip (Fig.53a) to those with a clavate tip (Fig.55a). Thus the length and structure of the ceratophore and style are useful specific characters. No other genus has papillated ceratophores, however some species of *Aphrodita* have small bulbous antenna covered with papillae.

b) Shape of prostomium. The shape of the prostomium is generally similar in all species of aphroditids examined, either round or oval. The development of ocular peduncles or raised ocular areas varies between genera. In *Aphrodita*, when eyes are present, the numbers of pairs may vary, some species in this genus also have low, raised peduncular areas. Eye pigment may fade over time as in the case of *A. malayana* Horst. Horst describes two pairs of eyes in 1917, while the same material today lacks any eye pigment.

Species of *Aphrogenia* have large ocular peduncles, and either possess or appear to lack eye pigment.

Similarly, species of *Laetmonice* possess ocular peduncles and may appear to completely lack eye pigment, or have two pairs of eyes which may or may not be of similar size. The ocular peduncles in *Pontogenia* vary in length, and in the small specimens of *P. araeoceras* (Haswell) the peduncles are fused to the median ceratophore. It is not clear if peduncle development is related to size or if this valuable generic character is taxonomically useful at the specific level. But the presence or absence of ocular peduncles is a useful generic character. However we regard the number of pairs of eyes in aphroditids as a poor character because of the tendency for the eye pigment to fade in alcohol. This is because that it appears that eye pigment in Aphroditids may be retained after a long period in preservative or may fade after such treatment. Thus although it may be a useful character in fresh material it may be a difficult one to interpret in preserved material because of distinguishing between species which lack eyes and those in which the pigment has completely faded and thus appear to lack eyes. This problem is a universal one which applies not within the Aphroditidae but in all polychaete families.

c) Nuchal flaps. The presence or absence of nuchal flaps is a useful means of distinguishing genera of aphroditids as they are absent in *Aphrogenia* and *Pontogenia*, and they may be present in *Laetmonice* and *Aphrodita*. As nuchal flaps are absent in most species of aphroditids, presumably the lack of flaps is a plesiomorphic character, but whether all nuchal flaps in the family are homologous is unknown at this stage.

5. Facial tubercle. The presence of a facial tubercle is a useful family character and the length of the facial tubercle appears constant for an individual species, although this may be affected by fixation. In addition the surface of the facial tubercle may be crenulated, or finely papillated, and we suggest that the ornamentation of the facial tubercle is another useful species character.

6. Palps. The length of the palps is a useful character and within a species fairly constant over a broad size range. The surface of the palps may be either smooth or finely papillated. We suggest that several distinct characters can be recognised. One character is the relative length of the palps and at least in *Laetmonice* three character states are present, short, medium and long. Another character is the ornamentation of the palps. In addition perhaps the shape and density of these papillae are additional specific characters. At this stage we suggest that these characters and their associated states are unordered.

7. Elytra. The number of pairs of elytra is fairly constant within the genus *Aphrodita* and *Pontogenia*, whereas within *Laetmonice* and *Aphrogenia* it varies between species. Elytra were dissected in species with a good development of felt only when the species was numerically well represented. The shape and the point of attachment to the elytrophore varies along the body, and may be diagnostic of a species. In *Laetmonice*, the structure appears similar in all species, although the species differ from each other in having different elytral structures in the last two pairs. In some species of *Aphrodita* the elytra do not completely cover the body leaving the caudal region exposed. However, because of the few individuals dissected, the usefulness of this character in *Aphrodita* is unclear.

The taxonomic value of the pigmentation of the elytra in *Aphrogenia* and its constancy over time with alcohol storage is unknown and should be assessed. The elytra appear to be fairly uniform in shape within *Aphrogenia*, however the ornamentation of the elytra may be a useful character in this genus.

The genus *Laetmonice*, exhibits the greatest range in the number of pairs of elytra present and ranges from 12 pairs in *L. batheia* Horst to 20 pairs in *L. producta* Grube, within the Indo-Pacific species (see Table 6). The number of pairs of elytra at least in *L. producta* appears to be constant (18 pairs) over a size range of 2.4 to 8.1 cm with the number of segments varying from only 41 to 45. However we did not examine sufficient material of a smaller size to ascertain if this was true for animals below 2.4 cm in length.

8. Parapodia. All species of aphroditids have the first segment with uniramous parapodia and subsequent

parapodia biramous with either a dorsal cirrus or elytrophore. Little if any change in parapodial structure occurs along the body or between species.

The relationships between the length of dorsal and ventral cirrus, differs between species. This could perhaps be quantified, although in species with a strong development of felt, measuring the dorsal cirrus would be difficult. The shape of the neuropodia of segments 2 and 3 of *Pontogenia* differs from subsequent neuropodia, and exhibits some difference between species, although this may be a result of the fixation.

9. Distribution and types of setae. *a) Notosetae.* Species of *Aphrodita*, *Aphrogenia*, *Laetmonice* and *Pontogenia* have several kinds of notosetae.

i) Capillary setae which may or may not form the dorsal felt. The thickness of the dorsal felt varies according to the species, presumably because of the density of capillary setae present. A felt is present in all species of *Aphrodita*, and *Heteraphrodita* whereas in *Laetmonice* and *Pontogenia* the development of the felt varies between species. A felt is completely absent in *Aphrogenia*. However, quantifying the development of felt in genera which possess one would be extremely difficult. Thus at least two character states exist; short capillary notosetae not forming a dorsal felt, and long capillary notosetae forming a felt. As a dorsal felt is absent in other genera of the family Aphroditidae and other families making up the order Phyllodocida (Fauchald, 1977) we suggest that the presence of a felt is an apomorphic state.

ii) Iridescent capillary setae. Iridescent setae are present in some species of *Aphrodita*. These setae vary in length and strength of iridescence and may project as a distinct lateral fringe in some species. All these characters are constant over a wide range of sizes within a species. To identify the lateral fringe as present or absent is relatively easy, however, the other features mentioned are not easily determined. The plesiomorph states of these features remain unknown. We have not been able to characterise the lateral fringe based on the density of the setae. The level of iridescence is maintained with storage of alcohol, however determination of the level of iridescence is fairly subjective so that character has a limited usefulness. In *Aphrogenia* fine capillary setae in a tuft of 100+ are present on the lower surface of both the elytrigerous and cirrigerous notopodia. This feature appears to be a good generic character, similarly, species of *Pontogenia* have short capillary setae arising on the ventral surface of the notopodia. The presence of these setae is a good generic character for *Pontogenia*.

iii) Acicular spines are present in *Aphrodita* and the number and structure of these acicular notosetae vary considerably between species and are good specific characters. The notosetae vary in structure from fine slightly iridescent ones, as found in *A. bamarookis* n.sp., to others in which the shafts are covered with small tubercles, as in *A. marombis* n.sp. Thus the following character states are recognised in *Aphrodita* (see Fig.1a): a) fine acicular setae, b) stout smooth with pointed tips, c) stout smooth with hooked tips, d) stout covered with tubercles with pointed tips, and e) stout covered with tubercles with hooked tips. Perhaps the plesiomorphic state is "a", and the apomorphic state "e". Another character is the number and distribution of acicular setae. The stout setae in *A. australis* Baird appear in two fascicles forming two distinct rows of setae along the lateral edge of the body, whereas the remaining species of *Aphrodita* examined have one fascicle only.

All species of *Laetmonice* possess simple acicular notosetae, which vary along the body and in *L. malayana* and *L. producta* numbers increase with increasing size and presumably age (see Tables 7, 8). We presume these acicular setae are homologous with those present in *Aphrodita*.

In *Pontogenia* the acicular spines are flattened, paleal in nature and their structure varies between species (see Fig.52c) and includes setae with long spines along one edge, covered in tubercles, or with denticles along the edge giving a serrated appearance. In addition the numbers of these spines on a particular segments may be a useful specific character in *Pontogenia*. It is unclear if the various types of acicular, sabre-like and harpoon notosetae present within these genera are homologous.

Species of *Aphrogenia* have stout, smooth sabre-like setae which curve over the dorsum. The number of sabre-like setae present on elytrigerous and cirrigerous notopodia vary between species and represent two useful characters. The structure of these setae differs among the Indo-Pacific species and at least two character states are present; smooth and ridged (Fig.27c). Those setae occurring on the cirrigerous notopodia are shorter than those on the elytrigerous notopodia. Whether setae of other species of *Aphrogenia* exhibit other character states is unknown. Presumably these setae are homologous with the acicular setae present in the other genera of aphroditids.

Finally, all species of *Laetmonice* possess harpoon notosetae with a series of recurved fangs on the lateral margins; the tip may be covered with a transparent sheath (Fig.32c). Shafts of harpoon notosetae vary, some are beset with spines, some tuberculated and some smooth. In *L. conchifera* (Horst) and *L. arenifera* (Horst), these notosetae are modified to form hook-like notosetae. However the number and arrangement of harpoon notosetae varies between species, and this may be a useful specific character. Harpoon notosetae are lacking in all other genera of the Aphroditidae, and within the order Phyllodocida and may represent the apomorphic state.

b) Neurosetae. Several different types of neurosetae occur.

i) Large number of bipinnate neurosetae are present in segments 2 to 3 in all species of *Aphrodita* (Fig.1d[8]) and at least in all Indo-Pacific species of *Aphrogenia* examined and in these two genera, the number and arrangement appears to vary very little from one species to the next. In *Laetmonice*, similar setae may be restricted to segments two and three, but may in some species be present on segment 4. In this genus, the number of

bipinnate setae present in upper and lower tier of neurosetae varies among species; we believe this feature to be a useful character in this genus. In *Pontogenia*, which has bipinnate setae in segments 2 to 3, the number and arrangement vary considerably among Indo-Pacific species; we believe these two features form useful specific characters in this genus. Pettibone (1966) stated that the bipinnate setae should be absent in *Pontogenia*, however we found them present in the species examined. Bipinnate setae are absent in *Heteraphrodita*.

ii) Stout neurosetae exhibit a range of variation within the family.

Laetmonice (Fig.32b[1-8]): (i) neurosetae with basal spur and distal fringe; (ii) neurosetae with basal spur and variety of additional teeth; (iii) neurosetae with basal spur and plumose edge.

Pontogenia (Fig.52b[1-3]): (i) stout with various levels of ornamentation.

Aphrogenia (Fig.27b[1-3]): (i) stout neurosetae.

Aphrodita (Fig.1d[1-8]): (i) stout neurosetae, smooth; (ii) stout neurosetae, with lateral spur; (iii) stout neurosetae, with or without slightly curved tips; (iv) stout neurosetae, with or without hood; (v) stout neurosetae, with hood which may be frayed or pilose.

We suggest that these neurosetae represent a single character with several character states but we do not know the plesiomorphic state. An additional character is the number of these setae present in each of the three tiers in anterior, middle and posterior parapodia. It also seems likely that this may vary according to the size of the individual in one or more tiers, and this may be species specific. This latter feature may make this character unsuitable for cladistic study, unless a large amount of material is available to determine the exact changes with increasing size and presumably age.

The relative lengths of neurosetae and notosetae in aphroditids is probably related to the method of fixation and therefore provides little useful information.

10. Other possible characters. In addition to these external characters, other useful characters may be the structure of the nephridial gonoducts and larval development but the material available did not allow an evaluation of these characters.

Taxonomic Account

Key to the Genera of Aphroditidae (* not recorded from Australia)

1. Dorsum covered with flattened fascicles of paleae ..... *Palmyra*

—— Dorsum covered with felted notosetae or elytra; paleae absent 2

2. Dorsum covered with felted notosetae; completely covering elytra 3

—— Dorsum without or with very few felted notosetae, elytra visible 4

3. With stout protective notosetae; prostomium without ocular peduncles; papillated facial tubercle well developed; neurosetae of anterior few segments bipinnate (Fig.1) ..... *Aphrodita*

—— Without stout protective notosetae; prostomium with short ocular peduncles; no facial tubercle; neurosetae of anterior few segments not bipinnate ..... *Heteraphrodita* *

4. Some stout protective notosetae with tips in form of barbed arrow (harpoon setae); neuropodia of anterior few segment with bipinnate neurosetae (Fig.32) ..... *Laetmonice*

—— Notosetae curved over dorsum; harpoon notosetae absent; neuropodia of anterior segments with or without bipinnate neurosetae 5

5. Notosetae sabre-like and smooth (Fig.27) ..... *Aphrogenia*

—— Notosetae flattened, marginally serrated or cylindrical and smooth 6

6. Notosetae flattened and marginally serrated (Fig.52) ..... *Pontogenia*

—— Notosetae cylindrical and smooth ..... *Hermionopsis* *

Aphrodita Linnaeus

Aphrodita Linnaeus, 1758: 655.–Pettibone, 1966: 96-97.
Aphroditella Roule, 1898: 191.–Horst, 1917: 4.

Diagnosis. Aphroditids with dorsal felt well developed, concealing elytra completely. Elytra 15 pairs, smooth. Prostomium without ocular peduncles, with or without nuchal flaps. Facial tubercle well developed, papillated. Notosetae all smooth, of 3 kinds: capillary setae forming matted dorsal felt; iridescent capillary setae projecting laterally; dark, acicular, protective spines projecting dorsolaterally. Neurosetae, dark, stout, smooth or with lateral spur, with slightly curved tips, with or without hood sometimes frayed or pilose. Neurosetae

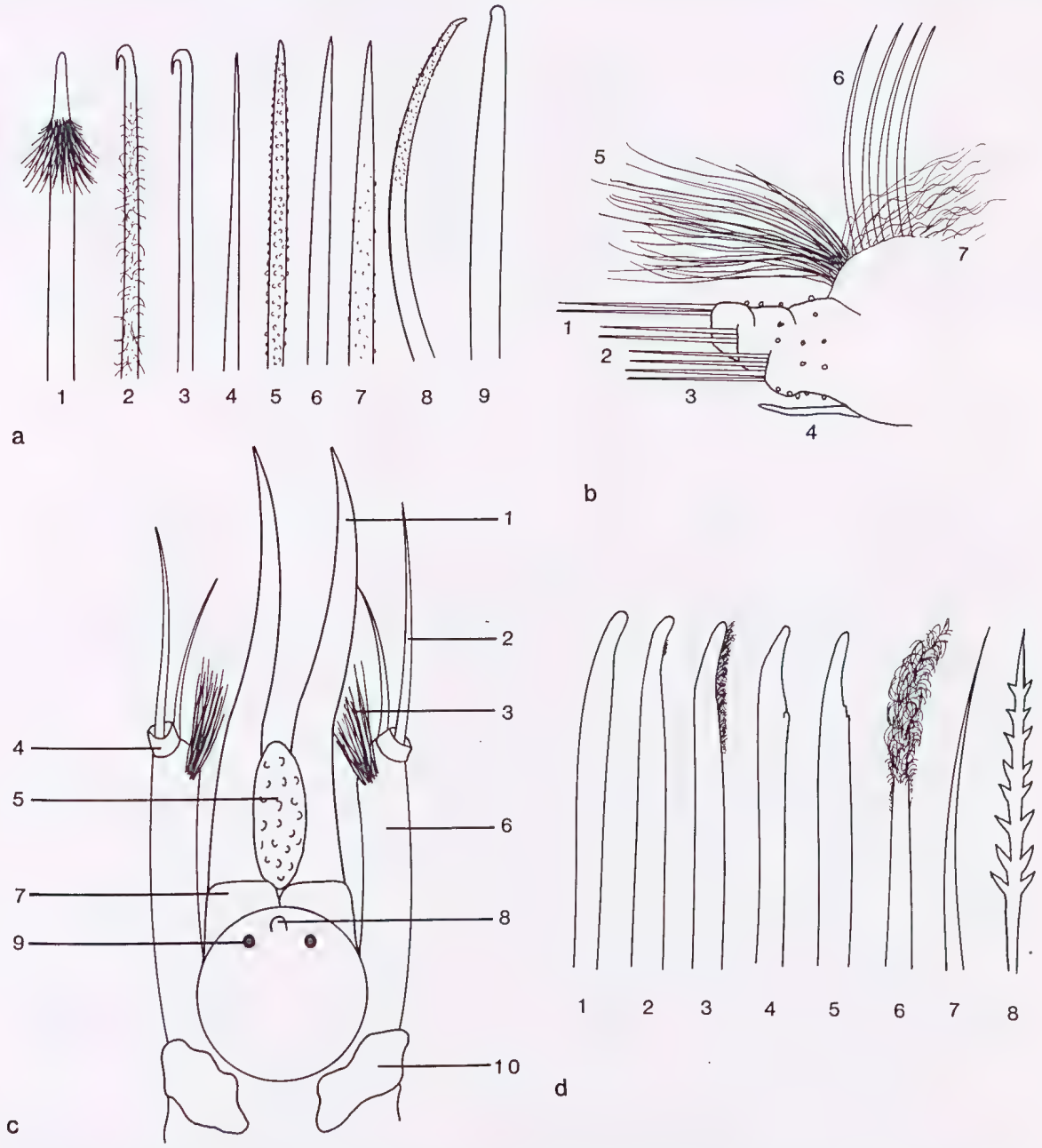

Fig.1. Generalised *Aphrodita*. a: notoseta types – 1, triangular tips with fine hairs radiating from expansion; 2, hooked tip with fine hairs and tubercles; 3, hooked tip, smooth; 4, acicular, smooth; 5, acicular, tuberculated; 6, spine, smooth; 7, spine, finely tuberculated; 8, bent with distal region densely tuberculated; 9, paleal-like, smooth. b: posterior view of parapodium – 1, upper tier of neurosetae; 2, middle tier of neurosetae; 3, lower tier of neurosetae; 4, ventral cirrus; 5, capillary notosetae; 6, acicular notosetae; 7, felt notosetae. c: dorsal view of prostomium and first segment – 1, palp; 2, tentacular cirrus; 3, setae; 4, tentaculophore; 5, facial tubercle; 6, first parapodium; 7, palpophore; 8, median antenna; 9, eye; 10, elytrophore. d: neuroseta types – 1, slightly curved tip; 2, slightly curved tip with small tuft of hairs on curved margin; 3, plumose margin; 4, slightly curved tip with small tubercle; 5, slightly curved tip with 2 small teeth; 6, pilose tipped; 7, extended tip; 8, bipinnate.

occurring in three tiers, upper tier with thicker neurosetae Some neurosetae of segments 2-3 bipinnate.

Type species. *Aphrodita aculeata*, designated by Malmgren, 1867.

Remarks. The above generic diagnosis is based upon that given by Pettibone (1966), although we have expanded the diagnosis to include the presence or absence of nuchal flaps to accommodate our new species. We believe that the following characters are important in defining species of *Aphrodita*: number of segments, presence or absence of stout notosetae, prostomial structure, length and shape of palps, size and shape of facial tubercle and median antenna which may be reduced to a papilla in some species (Kudenov, 1975), type of neurosetae, and development of capillary notosetae. A generalised figure of *Aphrodita* is given in Figure 1 together with the types of setae present. In many of the descriptions of *Aphrodita* detailed information on the characters we consider important in defining species of *Aphrodita* are not given and Hartman (1959, 1965) indicates that many species originally described as *Aphrodita* do not belong to this genus. Hartman (1959, 1965) and Hutchings (personal records) list 26 species of *Aphrodita*. Of these, four are described from the Indo-Pacific – *A. australis* Baird, 1865, *A. japonica* Marenzeller, 1879, *A. sondaica* Grube, 1875 and *A. watasei* Izuka, 1912 – and in addition *A maorica* Benham, 1900 has been described. The type of *A maorica* Benham appears to have been lost, and Benham's brief description is inadequate to define the species without the type material. All these descriptions are fairly brief, but we have included them in Table 1, indicating the characters which were given in the original descriptions, and in the case of *A. australis* an expanded description is given. A comprehensive revision of *Aphrodita* would require examination of all species currently assigned to the genus and is beyond the scope of this paper. However, in the introduction of this paper we consider in detail the characters useful in the diagnostic of species of *Aphrodita*.

Key to the Indo-Pacific Species of *Aphrodita*

1. Pair of nuchal flaps on posterior edge of prostomium (Fig.13a) ..... *Aphrodita kulmaris* n.sp.

—— Prostomial flaps absent 2

2. Notosetae with triangular shaped tips with fine hair-like spines radiating from base of expansion (Fig.19k) ..... *Aphrodita malkaris* n.sp.

—— Notosetae without triangular shaped tips 3

3. Neurosetae smooth, with slightly curved tips (Fig.3c-k) 4

—— Neurosetae with pilose tips (Fig.11e-j), plumose margin (Fig.24b-j) or ending in fine thread (Fig.6b-f) 6

4. Notosetae short, straight, covered with small tubercles (Fig.22k) ..... *Aphrodita marombis* n.sp.

—— Notosetae smooth (Fig.26f) 5

5. Felt thin; notosetae large paleal-like (Figs 25b, 26f), covering dorsum ..... *Aphrodita terraereginae*

—— Felt thick; notosetae thin, some entangled amongst felt, not covering dorsum ..... *Aphrodita australis*

6. Neurosetae ending in fine thread (Fig.6b-f) ..... *Aphrodita bamarookis* n.sp.

—— Neurosetae with pilose tips (Fig.11b-j); plumose margin (Fig.24b-j) 7

7. Neurosetae with pilose tips (Fig.11e-j); 14-26 neurosetae per neuropodium; palps extending to segments 7-11; eye pigment absent ..... *Aphrodita goolmarris* n.sp.

—— Neurosetae with plumose margin (Fig.24b-j) 8

8. Notosetae with distal halves densely tuberculated with hooked tips, shafts bent (Fig.8c) ..... *Aphrodita floresiana*

—— Notosetae with hooked tips, distal regions with fine tubercles and hairs (Fig.7c), or thick spines with shafts finely tuberculated (Fig.16b) 9

9. Notosetae with hooked tips, distal regions with fine tubercles and hairs (Fig.7c) 10

—— Notosetae thick spines with shafts finely tuberculated (Fig.16b) ..... *Aphrodita malayana*

10. Prostomium with raised hemispherical ocular areas, no eye pigment, 12-13 neurosetae per parapodium ..... *Aphrodita limosa*

—— Prostomium with raised ocular areas (Fig.23a), 2 pairs of eye spots 11

11. 7-8 neurosetae per parapodium, palps extending to segment 6 ..... *Aphrodita decipiens*

—— 10-15 neurosetae per parapodium; palps extending to segment 3-5 ..... *Aphrodita talpa*

Aphrodita australis Baird

Figs 2a-f, 3a-m, 59A, Tables 1, 2

Aphrodita paleacea Peters, 1864: 369-371.
Aphrodita australis Baird, 1865: 176-177.–Haswell, 1883: 270-271.–McIntosh, 1885: 34-36, pl.VII, figs 6,7, pl.VIa, figs 4-7.–Fauvel, 1917: 165-167, fig.1.
Aphrodita haswelli Johnston, 1909: 241-245, pl.LXIX figs 1-8.

Type material examined. HOLOTYPE of *A. australis*: Australia: South Australia: Port Lincoln, 34°44'S 135°52'E (BMNH 1865:12:23.2), 10.1 cm long.

Additional material examined. WESTERN AUSTRALIA: Port Hedland, 20°18'S 118°35'E, 26 Aug. 1983 (AM W20185), 1.2 cm long; Shark Bay, 25°25'S 113°35'E, Sept. 1963 (WAM 52-75), 5.5 cm long; Mullalloo, 31°47'S 115°44'E, 4 June 1962 (WAM 28-75), 5.5 cm long; Little Island, 31°49'S 115°43'E, 10 Feb. 1973 (WAM 27-73), 15 cm long; Watermans Bay, 31°51'S 115°45'E, 30 Aug. 1965 (WAM 1-75), 10.5 cm long; Trigg Island, 31°52'S 115°45'E, 24 Oct. 1985 (WAM 136-86), 7.5 cm long; Cottesloe, 31°59'S 115°45'E, 1975, 8(WAM 59-75), 4.5-14 cm long; Rottnest Island, 32°00'S 115°30'E, 15 May 1960 (NMV F57194), 14 cm long; Fremantle, 32°03'S 115°44'E, 1917 (WAM 2-75), 12.5 cm long; Woodman Point, 32°08'S 115°44'E, 1967 (WAM 3-75), 10 cm long; Garden Island, 32°12'S 115°40'E, 26 Nov. 1963 (WAM 55-75), 12.5 cm long; Bunkers Bay, 33°32'S 115°02'E, 31 July 1971 (WAM 6-74), 8.5 cm long; Dunsborough, 33°36'S 115°06'E, 28 June 1969 (WAM 96-89), 3.5 cm long; Bremer Bay, 34°24'S 119°26'E, 6 Aug. 1984 (WAM 82-89), 9.5 cm long; Mistaken Island, 35°03'S 117°58'E, 21 July 1963, 31 m (WAM 23-75), 1.4 cm long. SOUTH AUSTRALIA: Saint Francis Island, 32°31'S 133°18'E, 30 Dec. 1975, 20-30 m (NMV F57195), 13 cm long; Coffin Bay, 34°28'S 135°19'E, 17 Jan. 1984, 51.2 m (SAM E2165), 5 cm long; Port Lincoln, 34°47'S 135°51'E, 18 Mar. 1969, 11-18 m (NMV F57073), 6 cm long; Marum Island, 34°31'S 136°15'E, 10 Jan. 1984 (SAM E2169), 13.8 cm long; Cape Elizabeth, 34°20'S 136°53'E, 7 May 1989, 27 m (SAM E2163), 4.1 cm long; Corny Point, 34°54'S 137°01'E, 1912, 2(SAM E2168), 9.8-12.5 cm long; Whyalla, 33°02'S 137°35'E, 1926 (SAM E388), 13.5 cm long; Wallaroo, 33°56'S 137°38'E, 26 Sept. 1956 (SAM E2166), 6.2 cm long; Kangaroo Island, 35°50'S 138°03'E, 1966, 2-3 m (AM W5927), 9.4 cm long; Brighton, 35°01'S 138°31'E, 1939 (SAM E2164), 10.2 cm long; Glenelg, 34°58'S 138°32'E, 12 Mar. 1951 (SAM E2167), 10.5 cm long; Robe, 37°10'S 139°45'E, 12 Nov. 1966 (NMV F57070), 9 cm long. VICTORIA: Portland, 38°21'S 141°36'E, 9 Jan. 1921 (NMV G1122), 4.7 cm long; Hastings, 38°18'S 145°11'E, 29 May 1915 (NMV G1121), 14 cm long; Phillip Island, 38°28'S 145°12'E, 31 Jan. 1967 (NMV F57071), 11 cm long; Walkerville, 38°52'S 145°59'E, Apr. 1953, 33 m (AM W3590), 7.4 cm long; Lakes Entrance, 37°53'S 148°00'E, 25 Jan. 1978 (NMV F57197), 19 cm long. TASMANIA: Devonport, 41°11'S 146°21'E, 17 June 1962 (NMV F57075), 8 cm long; Flinders Island, 40°13'S 148°15'E, 2 Dec. 1970 (AM W4899), 10 cm long. NEW SOUTH WALES: Twofold Bay, 37°05'S 149°54'E, Feb. 1955, 11 m, 3(NMV F57072), 3.2-4 cm long; Botany Bay, 34°00'S 151°11'E, (AM W3183), 19 cm long; Middle Harbour, 33°45'S 151°11'E, 3 Mar. 1977, 2(AM W20168), 8.9-9 cm long; Port Jackson, 33°50'S 151°17'E, 11 m (AM W2693), 9 cm long; Balmoral, 33°03'S 151°35'E, 4 July 1901 (AM W20184), 3.4 cm long. A selection of the material examined.

HOLOTYPE of *A. haswelli*. Australia: New South Wales: Nelson Bay, 32°44'S 152°09'E, 1883, 9.1 m (AM G11394), 7.5 cm long.

TYPE of *A. paleacea*. Australia: South Australia: Gawler Bay, 34°56'S 138°36'E (ZMB 331).

Description. Based upon holotype of *A. australis*, except for description of first tentacular segment and elytra, based upon the holotype of *A. haswelli* (AM G11394). Body ovate, 10.1 cm long, 5.1 cm wide, caudal region attenuated, 42 segments.

Dorsum covered in thick felt, dark grey in alcohol. Capillary notosetae iridescent, green in alcohol, forming lateral fringe extending well beyond neurosetae. Some stouter golden brown notosetae over dorsum. Ventral surface light brown, covered with rounded papillae.

Prostomium (Fig.2a) small, rounded with pair of dark grey eyes. Median antenna reduced to a small, spherical papilla. Palps weakly biarticulate, extending to sixth to eighth segment, stout basal palpophores, palps, long, tapering, minutely papillated. Facial tubercle, wedge-shaped, length of prostomium, surface covered in rounded papillae.

Elytra 15 pairs, with firm stout attachments to elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra smooth, opaque. First pair of elytra, small, ovate, with elytrophore attached laterally, second pair rounded with elytrophore attached posterolaterally, third pair rounded with elytrophore attached anterolaterally. Subsequent elytra increasing in size to middle of body, then decreasing in size posteriorly, squarish with rounded edges, with elytrophore attachments on lateral margin. Posterior 2 pairs elongated. Elytrophore on terminal pair attached

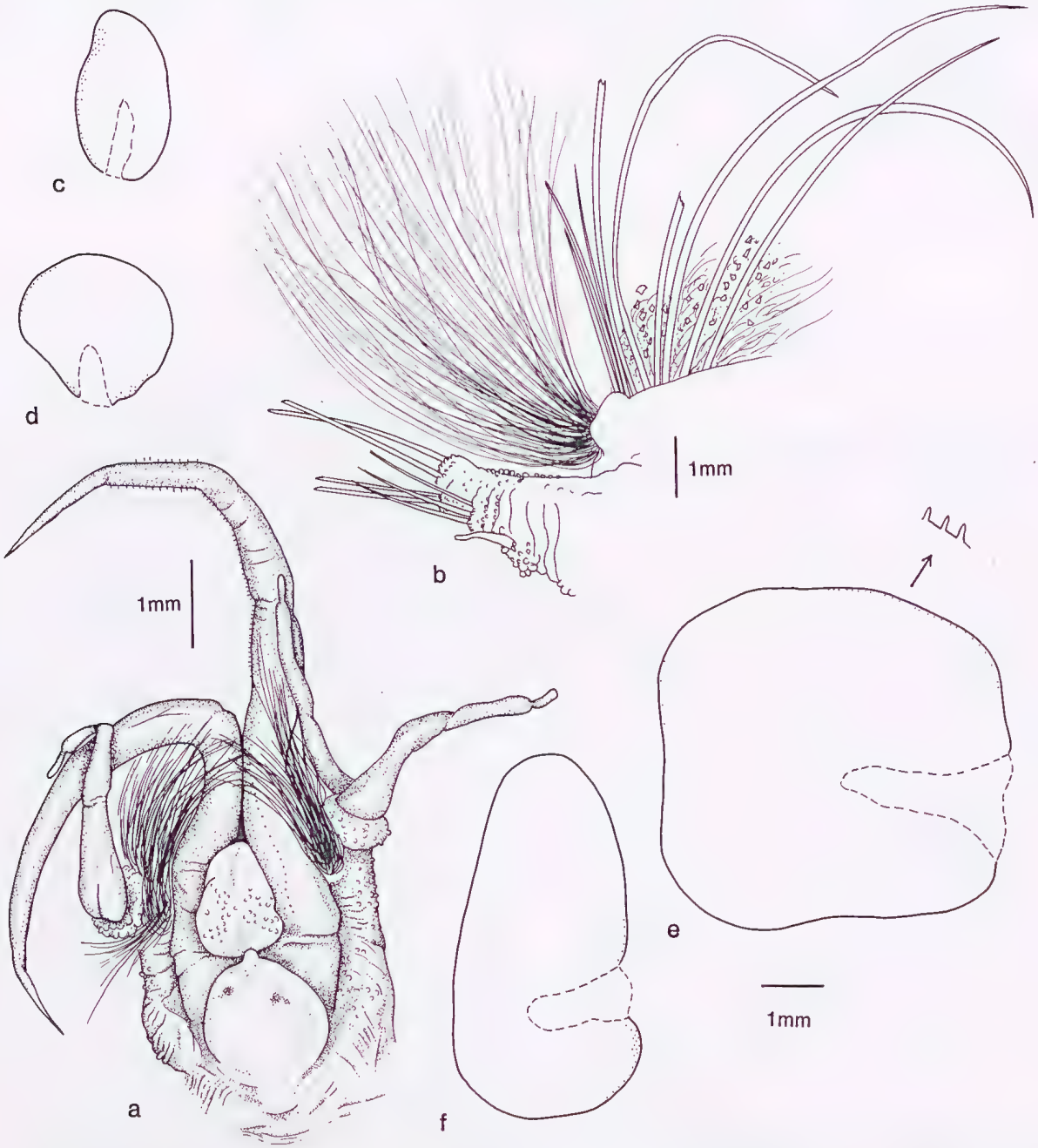

Fig.2. *Aphrodita australis*. Holotype (BMNH 1865: 12:23.2): a, dorsal view of prostomium and first segment; b, (WAM 6-75) posterior view parapodium from segment 15; c, (AM G11394) first elytron; d, third elytron; e, eighth elytron; f, 14th elytron.

anteriolaterally. All elytra with a few sub-marginal micropapillae (Fig.2c-f).

First or tentacular segment (Fig.2a) with elongated, uniramous parapodia covered with scattered globular papillae, projecting laterally and anteriorly to prostomium; with aciculae and several radiating bundles of capillary setae; 2 pairs of tentacular cirri, with large rounded tentaculophores, styles elongated, tapering, with small clavate tips, dorsal pair half length of palps, ventral pair just shorter than dorsal pair. Junction between tentaculophore and style poorly developed.

Following segments with biramous parapodia. Second segment with first pair of elytra attached on elongated elytrophore (Fig.2a). Neuropodia cylindrical covered with globular papillae; aciculae in middle part of lobe, with distal tip emerging between upper 2 neurosetae; neurosetae in 3 tiers; upper tier of 2 neurosetae longer, stouter, reddish-brown, smooth with slightly curved tips; middle tier of 2 neurosetae golden brown, smooth with slightly curved tips; lower tier of numerous (100+) neurosetae bipinnate, golden yellow (Fig.3a). Ventral cirri with large basal cirrophore, style tapering distally, with clavate tip, extending beyond distal margin of neuropodia. Notopodia squat, rectangular, on posterior face of neuropodia, small lobe with fascicle of capillary notosetae radiating around it; 2 fascicles of unidentate, golden brown notosetal spines; upper fascicle stronger, less numerous than lower fascicle, above dorsal fascicle tuft of felt notosetae. Third segment similar to second but carries long dorsal cirri, instead of elytra.

Following parapodia similar (Fig.2b). Neurosetae unidentate with slightly curved tips; occurring in 3 tiers: upper tier with 2 neurosetae (Fig.3e,h,k), middle tier with 2 neurosetae (Fig.3d,g,j), lower tier with 3-4 neurosetae (Fig.3c,f,i), upper ones stouter, thicker and darker than lower ones. Neurosetae of lower tier of anterior segments with some small denticles (Fig.3b). Ventral cirri extending to base of middle tier of neurosetae. Notosetae smooth, entangled amongst felt, curved over dorsum, some meeting in midline. Notosetae occurring in 2 fascicles, upper with 7-8 notosetae, lower with 9-10. Dorsal cirri with stout cirrophores, long slender tapering styles, with clavate tips, not extending beyond lateral fringe.

Variation. Additional material examined ranging from 1.4-19 cm long, and from 0.8-7.5 cm wide. Number of segments ranging from 41-45. Dorsum ranging in colour from pale brown or grey to dark grey/brown in alcohol. Lateral fringe cream coloured and faintly iridescent in alcohol in some specimens. Ventral surface varying from cream to light brown, dark brown and some of these with faint orange tinge.

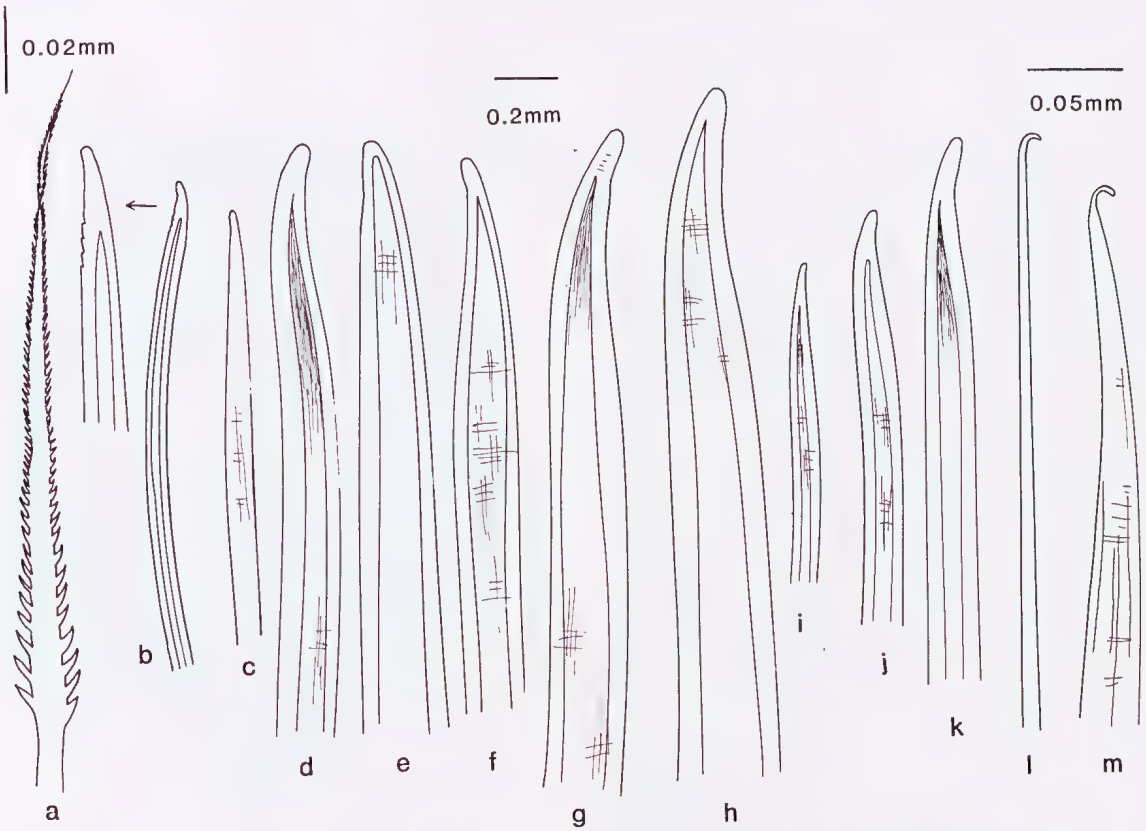

Fig.3. *Aphrodita australis*. Holotype (BMNH 1865: 12:23.2): a, bipinnate neuroseta from segment 3; b, (AM G11394) neuroseta with tubercles from lower tier segment 4; c, neuroseta from lower tier segment 4; d, neuroseta from middle tier segment 4; e, neuroseta from upper tier segment 4; f, neuroseta from lower tier segment 15; g, neuroseta from middle tier segment 15; h, neuroseta from upper tier segment 15; i, neuroseta from lower tier segment 30; j, neuroseta from middle tier segment 30; k, neuroseta from upper tier segment 30; l, tip notoseta (AM G11394) middle segment; m, tip notoseta.

Eyes varying from 1-2 pairs, some specimens with 2 pairs of contiguous eyes. Palps variable in length, reaching segment 5-8. Facial tubercle ranging from three-quarters the length of prostomium to just longer than prostomium. Median antenna reduced to a small papilla on all material examined, no evidence that this represents the ceratophore and that the style is missing.

In Table 2, the range in numbers of neurosetae present in each tier on segments 4, 15 and 25 for 4 size classes of *A. australis* are given. These counts indicate that the number of neurosetae in each tier does not increase with increasing size and presumably age of the individual, except perhaps for the inner tier which shows the greatest variation within a size class, and a slight tendency for numbers to increase in posterior segments with increasing size. Neurosetae of some specimens very short, only curved tip visible. Maximum length of thick upper neurosetae one and one half times length of parapodia. This variation may be due to the retraction of setae on fixation and the age of setae, as setae are regularly replaced with age.

Notosetae varying greatly in amount of dorsum they cover, ranging from half to whole dorsum, in some cases notosetae overlapping on mid-line of dorsum. Notosetae varying in thickness, some finer notosetae with small hooked tips (Johnston, 1909: pl.LXIX fig.7), (Fig.3lc). Notosetae of some specimens curving over top of dorsum and not entangled amongst felt.

Remarks. It had previously been reported that some juvenile *Aphrodita* have plumose neurosetae (Ushakov, 1955). The specimen of *A. australis* described by McIntosh (1885) had this type of neurosetae; however this animal was small, 2.6 cm long. All the material examined in this study, including the holotype, lack plumose neurosetae. Some of the Australian material examined was smaller than that examined by McIntosh, the smallest being 1.2 cm long and even this small individual had unidentate setae. It is unclear whether recently settled individuals possess plumose setae which are later replaced by unidentate setae, or if McIntosh was mistaken in his observation, or if his material represents another species. McIntosh's material was collected from Port Jackson, Sydney and other species of *Aphrodita* are known to occur in this area, *A. goolmarris* n.sp. and *A. kulmaris* n.sp. which have pilose tipped neurosetae. The original description by Baird (1865) states that all neurosetae were simple.

Although the type of *A. palaecea* Peters 1864 (ZMB 331) is dehydrated and therefore examination of all structures is not possible, we have synomymised *A. palaecea* Peters with *A. australis* for the following reasons. *Aphrodita australis* occurs widely in South Australia, including areas close to Gawler Bay the type locality of *A. palaecea*. No other Australian species of *Aphrodita* reaches the dimensions of *A. australis* and the type of *A. palaecea* was of similar dimensions to large specimens of *A. australis*, and the notosetae and neurosetae exactly matched those of *A. australis*. Although Peters' name has priority, by one year, we can find no other record of his name *A. palaecea* having being used, other than the original description. The name *A. australis* has been used widely in Australia and New Zealand (see Day & Hutchings, 1979) and we are suggesting that the name *A. australis* be retained, under Article 79c of the International Code of Zoological Nomenclature 1985, Third Edition and we are preparing a submission to the Commission to substantiate this (Hutchings & McRae, in preparation). Also amongst the type material of *A. palaecea* are two members of the family Polynoidae, Peters made no mention of these two polynoids living in association with *Aphrodita* and perhaps they were added to the jar subsequently.

The holotype of *A. haswelli* Johnston agrees well with the holotype of *A. australis* Baird and for these reasons we consider the two species synonymous.

Habitat. The material examined was found amongst sand, mud, algae and mussels. Most specimens had sand and shell fragments trapped in amongst their felt. Found at depths of 2 to 60 m. Many of the specimens were found washed up on beaches, and are therefore without habitat or depth information.

Distribution. Australia (Port Hedland, WA, 20°18'S 118°35'E, to Balmoral, NSW, 33°03'S 151°35'E, Fig.59A). Also from Japan, Sagami Bay* (Izuka, 1912), USSR, far eastern seas* (Ushakov, 1955), New Zealand, Petre Bay* (Knox, 1960).

Aphrodita bamarookis n.sp.

Figs 4, 5a-f, 6a-f, 59B, Table 1

Type material examined. HOLOTYPE: Australia: Victoria: Waratah Bay, 38°51'S 146°04'E, 20 Mar. 1969 (NMV F57074), 6 cm long, 3.2 cm wide, 51 segments. PARATYPES: South Australia: Saint Francis Island, 32°24'S 133°30'E, 5 May 1973, 42 m (USNM 148658), 5.5 cm long, 2.2 cm wide, 52 segments; Waldegrave Island, 33°36'S 134°47'E, 4 Apr. 1974 (AM W14123), 3.6 cm long, 1.8 cm wide, 51 segments; Noarlunga, 35°11'S 138°30'E, 19 Sept. 1965, 200 m (BMNH ZB1990.20), 5 cm long, 2 cm wide, 49 segments.

Additional material examined. WESTERN AUSTRALIA: Shark Bay, 25°25'S 113°35'E, Aug. 1965 (WAM 21-75), 3 cm long. SOUTH AUSTRALIA: Saint Francis Island, 32°31'S 133°18'E, Jan. 1975 (NMV F57190), 4.4 cm long; Venus Bay, 33°12'S 134°40'E, 1982 (SAM E2377), 4.1 cm long. VICTORIA: Waratah Bay, 38°51'S 146°04'E, 20 Mar. 1969 (NMV F57192), 5 cm long. NEW SOUTH WALES: Twofold Bay, 37°05'S 149°54'E, Feb. 1955, 11 m (NMV F57189), 3.8 cm long.

Description. HOLOTYPE. Body ovate, rounded anteriorly, long tapering caudal region forming a tail, 6 cm long, 3.2 cm wide, 51 segments (Fig.3).

Dorsum cream coloured in alcohol, covered in fine felt, with sand entrapped in felt giving grey appearance. Iridescent lateral fringe, creamy pink, extending well past neurosetae, forming margin around lateral edge of animal. No stout notosetae present. Ventral surface pale grey, crenulated, appearing smooth, but covered with fine spherical papillae.

Prostomium, small, rounded with 1 pair of faint grey eye spots. Median antenna reduced to small, rounded papilla, no style present on any of the material examined. Palps extending to segment 6 with large basal palpophores, stout, tapering, smooth. Facial tubercle, length of prostomium, inflated, covered in small globular papillae (Fig.5a).

Elytra 15 pairs (based on dissected paratype), firmly attached to elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra smooth, white, semi-transparent, first pair oval, with elytrophore attached centrally (Fig.5c), second pair rounded with elytrophore attached laterally. Remainder of elytra rounded with elytrophores attached laterally and slightly anteriorly (Fig.5d-f). Last 2 pairs of elytra elongated covering caudal region, leaving posterior tip uncovered.

First or tentacular segment with elongated uniramous parapodia, projecting anteriorly and laterally to prostomium, with aciculae and 3 tufts of iridescent, capillary setae: 2 emerging adjacent to tentacular cirri on dorsal and ventral surface, third emerging ventrally adjacent to the mouth. Two pairs of tentacular cirri, with cylindrical tentaculophores, styles tapering with slender tips. Dorsal and ventral cirri subequal in length, just shorter than parapodia (Fig.5a).

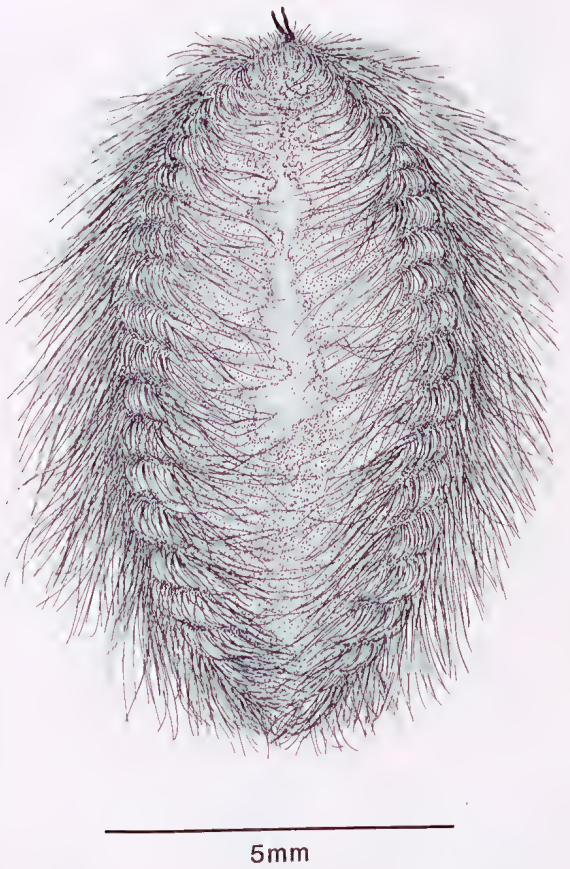

Fig.4. *Aphrodita bamarookis* n.sp. (NMV F57189): dorsal view, whole animal.

Second segment with first pair of elytra on large elytrophores (Fig.5a), parapodia biramous, neuropodia cylindrical, tip of acicula visible between upper 2 neurosetae. Neurosetae in 3 tiers; upper consisting of 2 neurosetae, golden, slender, ending in fine thread; middle neurosetae of 6 golden yellow, ending in fine thread; lower tier of numerous (100+) bipinnate neurosetae (Fig.6a). Ventral cirri with basal cirrophore, style tapering to slender tip, extending beyond distal tip of neuropodia. Notopodia rectangular with tuft of felt notosetae and fan of fine slender notosetae tapering to hooked tips, slightly iridescent, pointing posteriorly, some curving over dorsum (Fig.6g). Ventral surface of notopodia with long iridescent capillary notosetae forming lateral fringe.

Third segment same as second, but with dorsal cirri instead of elytra. Dorsal cirri long, slender tapering to blunt tip, just shorter than fringe.

Following segments with biramous parapodia (Fig.5b). Neurosetae, all ending in fine threads, occurring in 3 tiers, upper with 2-3 thicker, stouter, darker neurosetae (Fig.6b,e), middle with 6-7 neurosetae (Fig.6c,f), lower with 15-17 neurosetae (Fig.6d). Notosetae covering three-quarters of dorsum, merging with iridescent lateral fringe.

Variation. Additional material examined ranges from 3-6 cm long and from 1.5-3.4 cm wide and 49-52 segments. Palps extending to segment 4 to 6. Facial tubercle three-quarters to 1 times length of prostomium. Neurosetae numbering 2-3 in upper tier, 4-7 in middle tier, and 9-17 in lower tier.

Remarks. *Aphrodita bamarookis* n.sp. can be distinguished from all the other species of *Aphrodita* recorded from the Indo-Pacific by its large number of segments, the presence of fine slightly iridescent notosetae and the long iridescent cream or pink lateral fringe. Stout notosetae are absent. The neurosetae are smooth and subulate and relatively large numbers are present in comparison to other known species (see Table 1). *Aphrodita bamarookis* n.sp. is currently only known from southern Australia and these above characters clearly distinguish it from other species of *Aphrodita*, *A. goolmarris* n.sp., *A. marombis* n.sp., *A. australis* and *A. talpa* which occur in southern Australian waters.

Habitat. No habitat information available, although sand and shell fragments were entangled amongst the felt of many of the individuals examined. Only

three specimens examined, had information as to the depths at which they were collected, these were at 11, 42 and 200 m. One specimen was found in the gut of a whiting.

Etymology. The specific name is from an aboriginal word *Bamarook* which means oval shield, and this species resembles one.

Distribution. Australia (southern Australia from Shark Bay, WA, 25°25'S 113°35'E, to Twofold Bay, NSW, 37°05'S 149°54'E, Fig.59B).

Fig.5. *Aphrodita bamarookis* n.sp. Holotype (NMV F57074): a, dorsal view of prostomium and first segment; b, posterior view parapodium from segment 15; c, first elytron; d, third elytron; e, eighth elytron; f, 14th elytron.

Aphrodita decipiens (Horst)

Figs 7a-c, 60, Table 1

Aphroditella decipiens Horst, 1916b: 66-67.–Horst, 1917: 50, pl.XI figs 11,12.
Aphroditella mongolica Horst, 1916b: 67.–Horst, 1917: 50-51, pl.XI figs 13-16.

Type material examined. HOLOTYPE: Indonesian Archipelago Stn 51: Molo Strait, 8°45'S 119°46'E, 69-91 m (ZMA V.Pol 69), 1 cm long, 0.85 cm wide, 35 segments.
HOLOTYPE of *A. mongolica*. Indonesian Archipelago Stn 105: north off Sulu Island, 6°8'N 121°19'E, 275 m (ZMA V.Pol 73), 2 cm long, 1.4 cm wide, 35 segments.

Description. Body ovate with attenuated caudal region, 1-2 cm long, 0.85-1.4 cm wide, 35 segments. Dorsum tan coloured in alcohol with thick sand encrusted felt. Ventral surface tan coloured, covered in spherical papillae.

Prostomium rounded with slightly raised hemispherical ocular area, with 2 pairs of small eye spots. Median antenna with short ceratophore one-quarter length of prostomium, style thin, one and one-quarter length of prostomium. Facial tubercle inflated, covered in small rounded papillae, half length of prostomium. Palps extending to segments 6-7, tapering, with minutely papillated margins (Horst, 1917: pl.XI fig.11).

First or tentacular segment with elongate, uniramous parapodia, projecting laterally and anteriorly to prostomium with tuft of mud-covered, capillary setae on medial and posterior edge; 2 pairs of tentacular cirri, with cylindrical tentaculophores, dorsal pair missing, ventral pair tapering, length of prostomium.

Following segments with biramous parapodia. Neuropodia of segments 2 and 3 short, with 2 tiers of neurosetae, lower with many (50+) pale yellow, bipinnate neurosetae (Fig.7a), upper tier with 2-3 golden yellow neurosetae with slightly curved tips (Fig.7b). Buccal cirri and ventral cirri from segment 3 with papillated cirrophore, styles clavate-tipped, extending past distal tip of neuropodia.

Remaining parapodia with neuropodia cylindrical, covered with small rounded papillae, with 3 tiers of stout, golden brown, neurosetae with plumose margin (Horst, 1917: pl.XI fig.12), upper tier with 2 stouter, darker neurosetae, middle tier with 2-3 neurosetae, lower tier with 3 thinner neurosetae. Ventral cirri clavate-tipped, extending to distal tip of neuropodia. Ventral surface of notopodia with short tuft of mud-covered, pale yellow, capillary notosetae, not forming conspicuous fringe. Upper notosetae about 20, varying in thickness with fine hooked tips, bases thick, smooth, distal halves with fine tubercles and fine hairs (Fig.7c), entangled amongst felt,

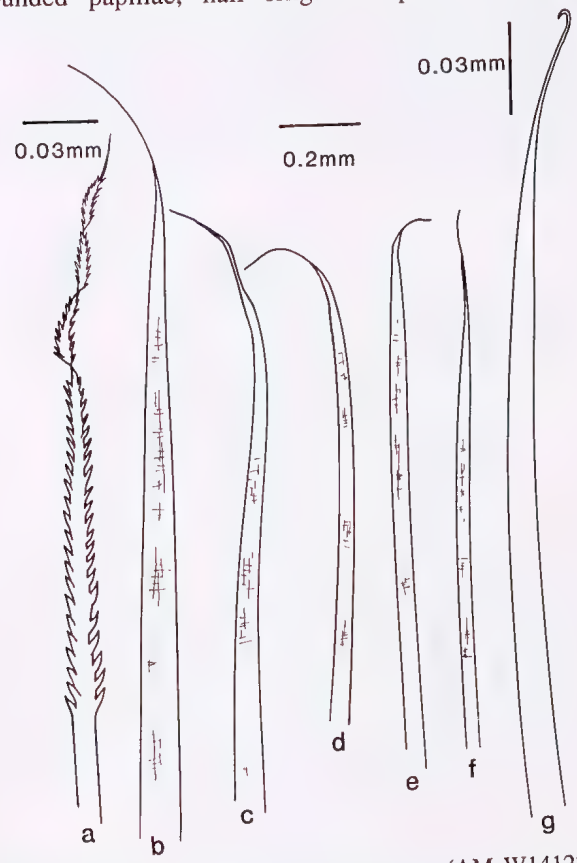

Fig.6. *Aphrodita bamarookis* n.sp. Paratype (AM W14123): a, bipinnate neuroseta from segment 3; b, neuroseta from upper tier segment 15; c, neuroseta from middle tier segment 15; d, neuroseta from lower tier segment 15; e, neuroseta from upper tier segment 25; f, neuroseta from middle tier segment 25; g, notoseta from middle segment.

Fig.7. *Aphrodita decipiens* (ZMA V.Pol 69): a, bipinnate neuroseta from segment 2; b, upper neuroseta from segment 2; c, tip of notoseta from middle segment.

curving over dorsum.

Remarks. Pettibone (1966) synonymised *Aphroditella* Roule, 1898 with *Aphrodita*, quoting that the type species of the genus *A. pallida* Roule, 1898 was a young form of *Aphrodita aculeata* Linnaeus, 1758 according to Fauvel, 1923 the type species of *Aphrodita* Linnaeus, 1758, as designated by Malmgren, 1867. Pettibone (1966) did not indicate the placement of the other species which have subsequently been placed in the genus *Aphroditella*. Roule (1898) described a new species of *Aphroditella pallida* without formally describing a new genus, although Horst (1916b) provides the following generic diagnosis, "Resembling *Aphrodita*; ventral bristles however not smooth, but pilose or pinnate". Pettibone (1966) regards this character as insufficient to maintain the genus *Aphroditella* and her generic diagnosis of *Aphrodita* includes variable neurosetae including smooth, frayed pilose and bipinnate neurosetae. We agree with this and all the species of *Aphroditella* described by Horst (1916b, 1917) and redescribed in this paper, clearly belong to the genus *Aphrodita*.

We have synonymised *A. mongolica* (Horst, 1916b) with *A. decipiens* as the holotype of these two species are identical. We have expanded the species description given by Horst (1916b, 1917) to include details of setal distribution and numbers.

The main characters which distinguish this species which is known only from the two specimens examined, from other Indo-Pacific species, are the presence of notosetae with hooked tips and with the distal regions of the shafts covered with fine tubercles and hairs, and seven to eight neurosetae per parapodium and palps extending to segment 6 (see Table 1).

Habitat. Collected at depths of 69 to 91 m and 275 m.

Distribution. Indonesian Archipelago (Fig.60).

Aphrodita floresiana (Horst)

Figs 8a-c, 60, Table 1

Aphroditella floresiana Horst, 1916b: 67-68.–Horst, 1917: 51, pl.XII figs 1-5.

Type material examined. LECTOTYPE: Indonesian Archipelago Stn 51: Molo Strait, 8°45'S 119°46'E, 69-91 m (ZMA V.Pol 70.2), 2.7 cm long, 1.5 cm wide, 34 segments. PARALECTOTYPES, Indonesian Archipelago Stn 51: Molo Strait, 8°45'S 119°46'E, 69-91 m (ZMA V.Pol 70.3), 0.6 cm long, 0.37 cm wide, 30 segments; Indonesian Archipelago Stn 153, north of Waigeu Island, 0°3.8'N 130°24.3'E, 141 m (ZMA V.Pol.70.1), 0.8 cm long, 0.54 cm wide, 28 segments.

Description. Body ovate, with attenuated caudal region, 0.8-2.7 cm long, 0.54-1.5 cm wide, 28-34 segments.

Dorsum with thick felt encrusted with sand, some grains black giving mottled tan appearance in alcohol. Ventral surface tan, covered with small spherical papillae.

Prostomium rounded with slightly raised hemispherical ocular area, with 2 pairs of small eye spots (faded, probably due to age). Median antenna with short ceratophore, style thin, three-quarters length of prostomium (style missing from holotype). Facial tubercle inflated, covered in small rounded papillae, length of prostomium. Palps extending to segments 6-7, large basal palpophores, palps, tapering, with minutely papillated margins (Horst, 1917: pl.XII fig.1).

Elytra 15 pairs, with firm stout attachments to elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra smooth, semi-transparent, first pair rounded with elytrophore attached centrally, second pair missing, remainder of elytra rounded with elytrophore attached laterally, posterior elytra elongated with elytrophores attached on anteriolateral margins.

First or tentacular segment with elongate, papillated, uniramous parapodia, projecting laterally and anteriorly to prostomium with tuft of mud-covered, capillary setae on medial and posterior edge; 2 pairs of tentacular cirri, with cylindrical tentaculophores, styles elongated, tapering, dorsal pair length of median antenna, ventral pair two-thirds length of dorsal pair.

Following segments with biramous parapodia. Neuropodia of segments 2 and 3 short, with 3 tiers of neurosetae, lower with many (100+) golden yellow, bipinnate neurosetae (Fig.8a), middle tier with 3, upper tier with 2 golden yellow neurosetae with slightly curved

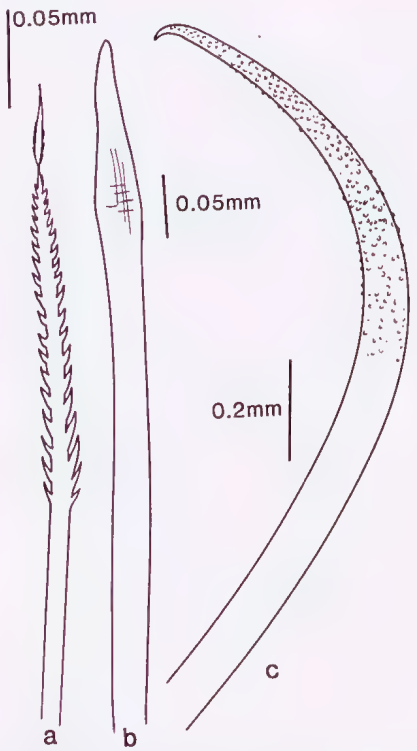

Fig.8. *Aphrodita floresiana* (ZMA V.Pol 70.2): a, bipinnate neuroseta from segment 3; b, upper neuroseta from segment 3; c, notoseta from middle segment.

tip (Fig.8b).

Remaining parapodia with neuropodia cylindrical, covered with small rounded papillae, with 3 tiers of stout, golden brown, neurosetae with plumose margin (Horst, 1917: pl.XII fig.4a,b), upper tier with 2 stouter, darker neurosetae, middle tier with 3-5 neurosetae, lower tier with 6-9 neurosetae. Some neurosetae of anterior segments smooth, without plumose margins. Ventral cirri clavate-tipped, extending to distal tip of neuropodia. Ventral surface of notopodia with short lateral tuft of mud-covered capillary notosetae, shorter than neurosetae, not forming conspicuous fringe. Dorsal surface of notopodia with 2 types of notosetae entangled amongst felt; medially a row of about 10, stout, slightly bent, golden yellow, densely tuberculated on anterior halves, with hooked tips curving over dorsum. (Horst, 1917: pl.XII figs 2,3); laterally a row of 10-15 sharply bent, golden yellow, densely tuberculated on anterior halves, with hooked tips (Fig.8c). Paralectotypes smaller than lectotype, possessing the sharply bent notosetae only. Dorsal cirri with cylindrical cirrophores on posterior edge of notopodia, styles clavate-tipped shorter than bent notosetae.

Remarks. The reasons for referring this species to *Aphrodita* are given in the Remarks section of *A. decipiens*. We have expanded Horst's original description slightly but have not dissected the type material to reveal the elytra. The main characters which clearly separate this species from all other species of *Aphrodita* in the Indo-Pacific is the lack of a notosetal fringe, the presence of raised ocular areas, and the few neurosetae present (see Table 1). The species is known only from the type locality.

Habitat. Collected at depths of 69 to 91 m and 141 m.

Distribution. Indonesian Archipelago (Fig.60).

Aphrodita goolmarris n.sp.

Figs 9, 10a-f, 11a-j, 59C, Tables 1, 3

Type material examined. HOLOTYPE: Australia: Western Australia: Rowley Shoals, 18°15'S 118°02'E, 22 Aug. 1983, 410 m (WAM 74-89), 5.4 cm long, 2.9 cm wide, 39 segments. PARATYPES: New South Wales: off Batemans Bay, 35°44'S 150°15'E, 549 m (USNM 148659), 4.8 cm long, 2.6 cm wide, 36 segments; off Batemans Bay, 35°44'S 150°15'E, 549 m (BMNH ZB1990.19), 5.8 cm long, 2.7 cm wide, 40 segments; Brush Island, 35°32'S 150°25'E, 457 m (AM W20174), 4.7 cm long, 2.5 cm wide, 39 segments.

Additional material examined. WESTERN AUSTRALIA: Rowley Shoals, 16°49'S 119°59'E, 19 Aug. 1983 (WAM 78-89), 5 cm long; scampi trawl grounds, 17°24'S 118°52'E, 4 Nov. 1985, 445 m, 2(NTM W4252), 4.4 cm long; scampi trawl grounds, 17°28'S 118°53'E, 8 Nov. 1985, 405 m (NTM W4254), 4.6 cm long; scampi trawl grounds, 17°52'S 118°27'E, 6 Nov. 1985, 420 m (NTM 4253), 5.5 cm long; Rowley Shoals, 17°56'S 118°26'E, 29 Aug. 1983, 400 m (WAM 75-89), 4.5 cm long; Rowley Shoals, 18°06'S 118°10'E, 17 Aug. 1983, 353-356 m (WAM 76-89), 4.5 cm long; Karratha, 18°44'S 116°59'E, 23 Aug. 1983 (WAM 84-89), 6 cm long. TASMANIA: Richardson Point, 41°15'S 144°08'E, 20 Oct. 1984, 520 m (SAM E2380), 3 cm long. NEW SOUTH WALES: Disaster Bay, 37°21'S 150°18'E, 14 Oct. 1984, 636 m (SAM E2379), 3.3 cm long; off Sydney, 34°24'S 151°25'E, 13 Dec. 1976, 731-768 m, (AM W20169), 4.2 cm long; Terrigal, 34°47'S 151°57'E, 7 Dec. 1978, 816 m (AM W20170), 3.5 cm long; off Newcastle, 32°56'S 151°46'E, 8 Oct. 1982, 2984-3058 m (AM W20374), 3 cm long. QUEENSLAND: Cape York, 10°29.81'S 144°00.38'E, 20 Aug. 1988, 495-534m (AM W20318).

Description. HOLOTYPE. Body ovate, 5.4 cm long, 2.9 cm wide, 39 segments.

Dorsum tan-brown in alcohol, stout golden brown notosetae entangled amongst felt, lateral fringe small inconspicuous (Fig.9). Ventral surface tan, covered with small spherical papillae.

Prostomium rounded with raised hemispherical ocular area, without eye pigment. Median antenna rod-shaped, one-fifth length of prostomium. Facial tubercle inflated, covered in small rounded papillae, length of prostomium. Palps extending to segment 11, large basal palpophores equal to length of prostomium, palps, long, tapering, with minutely papillated margins (Fig.10a).

Elytra 15 pairs attachments by elytrophores on

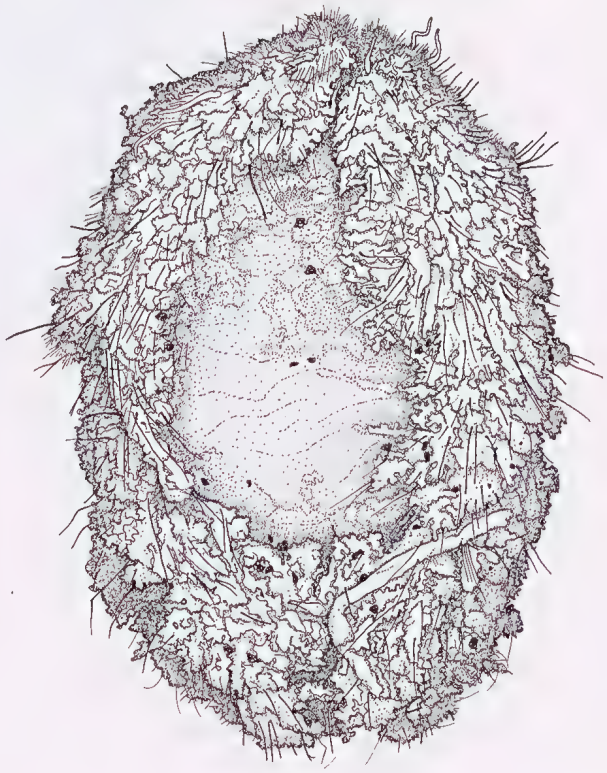

Fig.9. *Aphrodita goolmarris* n.sp. (AM W20374): dorsal view, whole animal.

segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. First pair rounded with elytrophore attached centrally. Remaining elytra rounded with elytrophores attached laterally, increasing in size to middle of body, then decreasing in size posteriorly. Posterior elytra ovoid with elytrophores attached anteriolaterally. All elytra with some scattered submarginal papillae (Fig.10c-f).

First or tentacular segment with elongated, flattened, uniramous parapodia, covered in small rounded papillae, anterior margin with 2 small tentaculophores and tentacular cirri, tapering with blunt ends, dorsal and ventral pair equal to length of prostomium. Three tufts of fine, pale, faintly iridescent, mud-covered setae; tuft on inner anterior edge of parapodia, tuft on distal margin of parapodia, and small tuft ventrally emerging posterior to cirri.

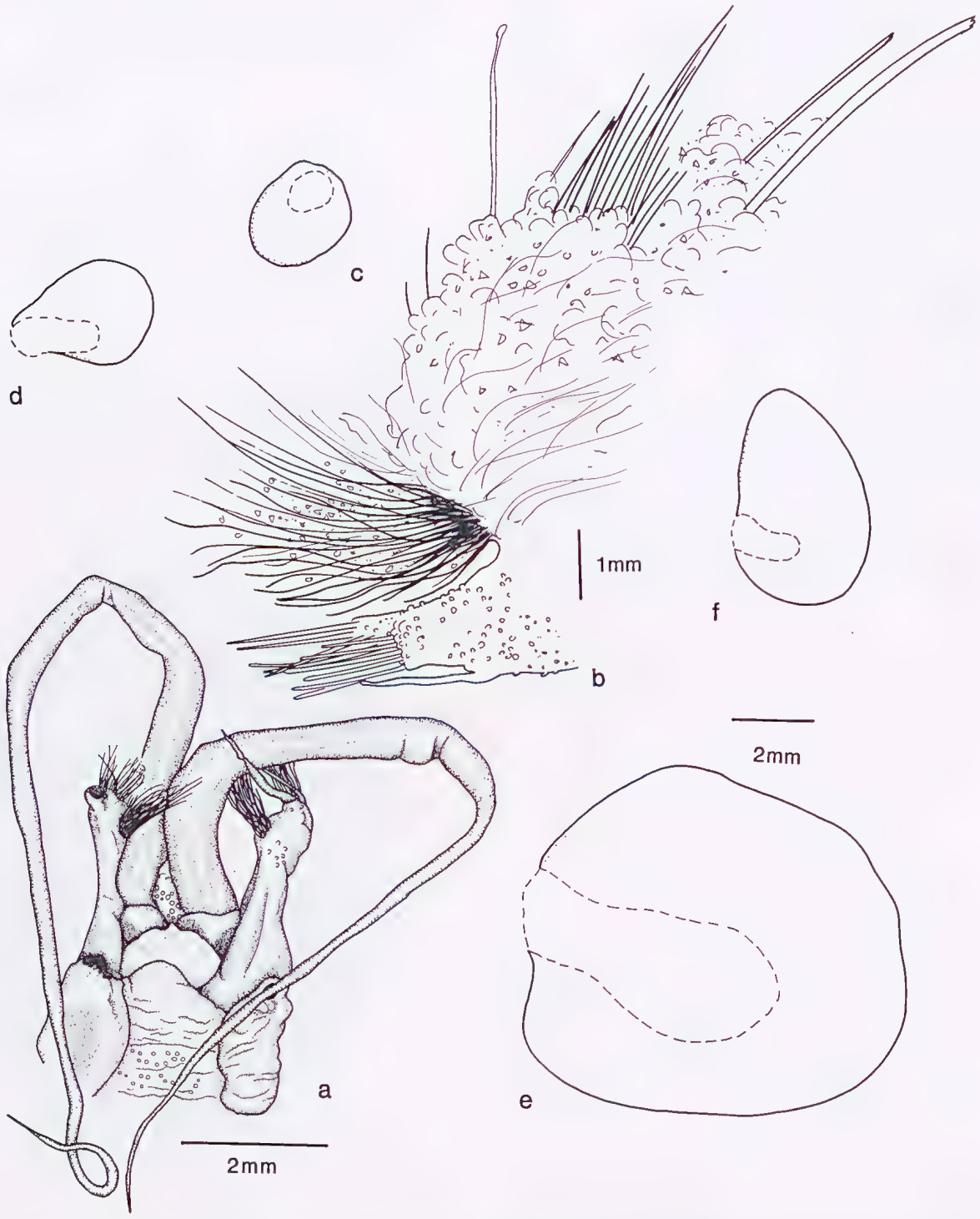

Fig.10. *Aphrodita goolmarris* n.sp. Holotype (WAM 74-89): a, dorsal view of prostomium and first segment; b, parapodium from segment 15; c, (AM W20174) first elytron; d, third elytron; e, eighth elytron; f, 14th elytron.

Following segments with biramous parapodia. Neuropodia of segments 2 and 3 short, cylindrical, covered in small papillae, with 2 tiers of neurosetae, upper with 2-3 golden brown, stout neurosetae, lower with many (100+) golden yellow, bipinnate neurosetae (Fig.11a). Ventral cirri slender, tapering, with blunt tips, extending to tip of neuropodia.

Remaining parapodia (Fig.10b) with neuropodia cylindrical, covered with small rounded papillae, with 3 tiers of stout, golden brown, pilose-tipped, neurosetae, upper tier with 2 stouter, darker neurosetae (Fig.11g,j), middle tier with 4-9 neurosetae (Fig.11f,i), lower tier with 8-15 neurosetae (Fig.11e,h). Neurosetae of some anterior segments without pilose tips (Fig.11b-d). Ventral cirri extending to lower tier. Notopodia with short lateral tuft of faintly iridescent, mud-covered capillary notosetae, not forming fringe, upper notosetae golden brown, entangled amongst felt, curving over half the dorsum (Fig.11k). Dorsal cirri with blunt tips, as long as notosetae.

Variation. Additional material ranges from 2.6-6 cm long, 1.0-4.6 cm wide, with segments 35-41.

Raised hemispherical ocular areas not pronounced in some specimens. Palps extending to segments 7-11, palps, long, tapering, with smooth margins, or finely papillated. Median antenna rod-shaped up to one fifth length of prostomium, in none of the material examined was their evidence that a style was originally present.

Ventral cirri extending from lower tier to middle tier of neurosetae. Some neurosetae plumose on margin only (usually large upper setae).

Three specimens from New South Wales with elongated neurosetae up to 2 times length of neuropodia.

In Table 3, the numbers of neurosetae present in each tier on segments 4, 15 and 25 are given for three size classes of individuals. While the number of neurosetae in the upper tier remains constant with increasing size, the number in the lower and middle tier increases with increasing size and presumably age. Also the number of setae in these 2 tiers (lower, middle) is not constant over the body with larger numbers of neurosetae present on segment 15 than on segment 4 or 25.

Remarks. *Aphrodita goolmarris* n.sp. is characterised by stout golden brown notosetae, pilose-tipped

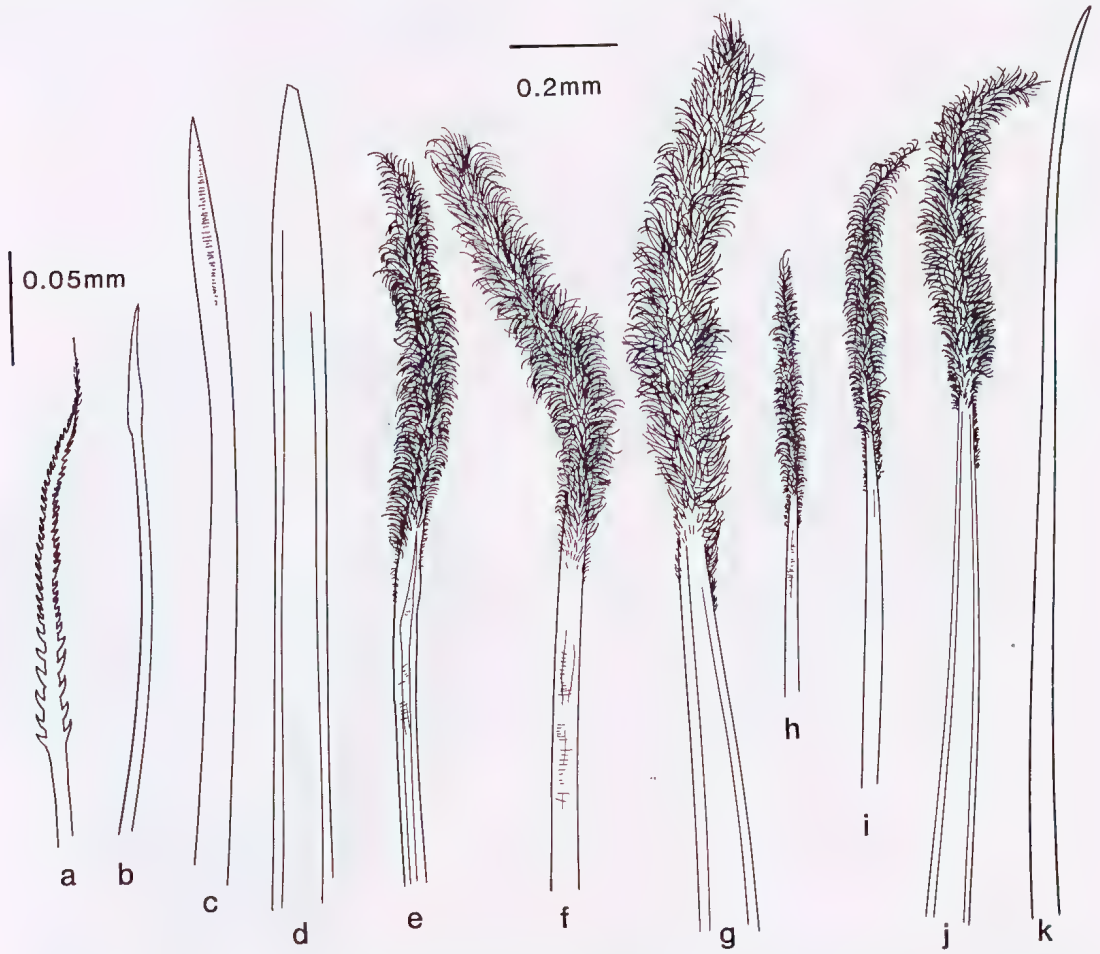

Fig.11. *Aphrodita goolmarris* n.sp. (AM W20169): a, bipinnate neuroseta from segment 3; b, neuroseta from lower tier segment 4; c, neuroseta from middle tier segment 4; d, neuroseta from upper tier segment 4; e, neuroseta from lower tier segment 15; f, neuroseta from middle tier segment 15; g, neuroseta from upper tier segment 15; h, neuroseta from lower tier segment 25; i, neuroseta from middle tier segment 25; j, neuroseta from upper tier segment 25; k, notoseta from middle segment.

neurosetae and a rod-shaped median antenna and as indicated in Table 1, no other species of *Aphrodita* from the Indo-Pacific has this combination of characters.

Aphrodita goolmarris n.sp. is known from Rowley Shoals in Western Australia, Tasmania, New South Wales and a single record from Queensland. Additional collecting may reveal that this species is more widespread.

Habitat. Found at depths of 353 to 3058 m.

Etymology. The specific name is from an aboriginal word *Goolmarry*, meaning a shield, as this species has the body form of a shield.

Distribution. Australia (from Rowley Shoals, WA, 16°49'S 119°59'E, to Cape York, Qld, 10°29.81'S 144°00.38'E, Fig.59C).

Aphrodita kulmaris n.sp.

Figs 12, 13a-f, 14a-l, 59B, Tables 1, 4

Type material examined. HOLOTYPE: Australia: Victoria: Lakes Entrance, 37°53'S 148°00'E, June 1962 (NMV F57193), 7.1 cm long, 4 cm wide, 43 segments. PARATYPES: New South Wales: Malabar, 33°58'S 151°15'E, 19 July 1972, 15.8-16.5 m (LACM-AHF 1299), 4 cm long, 3.5 cm wide, 42 segments; Manly, 33°48'S 151°17'E, 124 m (USNM 148660), 5.5 cm long, 3 cm wide, 44 segments; Newcastle, 33°13'S 152°11'E, 76.8-87.8 m (AM W20172), 5 cm long, 2.5 cm wide, 43 segments. Queensland: Flinders Island, 14°09'S 144°04'E, 26 Feb 1979, 22-28 m (BMNH ZB 1990.21), 3.9 cm long, 1.7 cm wide, 42 segments.

Additional material examined. WESTERN AUSTRALIA: Long Reef, 13°50'S 125°00'E, Nov. 1980, 2(WAM 92-89), 5.5-8 cm long; North West Cape, 15°00'S 124°00'E, 121-128 m (WAM 10-75), 8 cm long; Broome, 17°58'S 122°14'E, 13 m (AM W2843), 8.2 cm long; Shark Bay, 25°31'S 112°29'E, 9 Oct. 1963, 130 m, 2(WAM 108-90), 2.5-4 cm long. VICTORIA: Gabo Island, 37°34'S 149°55'E, 119 m (AM W3497), 5.5 cm long. NEW SOUTH WALES: Green Cape, 37°16'S 150°03'E, 20 July 1925, 55 m (AM W1741), 4.7 cm long; Tathra, 36°49'S 149°57'E, Mar. 1927, 73 m (AM W2363), 5.8 cm long; Ulladulla, 35°21'S 150°29'E, 73-82 m (AM W3177), 2.5 cm long; Cronulla, 34°02'S 151°09'E, 17 June 1965 (AM W20176), 2 cm long; Botany Bay, 34°00'S 151°11'E, Sept. 1921, 60-102 m, 3(AM W854), 3.5-5.5 cm long; Malabar, 33°58'S 151°15'E, 26 Mar. 1973, 66 m (AM W6881), 3.6 cm long; Broken Bay, 33°36'S 151°30'E, 10 Feb. 1986, 71-75 m, 3(AM W20177), 1.8-2 cm long; Newcastle, 33°13'S 152°11'E, 7 Dec. 1977, 146 m (AM W20178), 4.5 cm long. QUEENSLAND: Cape Moreton, 27°02'S 153°28'E, 30 Mar. 1969, 2(QM GH2850), 3.2-4 cm long; Yepoon, 23°08'S 150°44'E, 6 Sept. 1967, 9 m (NMV F57187), 3 cm long; Bowen, 20°01'S 148°15'E, 11 June 1983, 22-26 m (AM W20179), 2.6 cm long; Abbot Point, 19°53'S 147°05'E, 1982, 5 - 10 m (QM G23030), 6.8 cm long; Townsville, 17°53'S 146°51'E, 20 Jan. 1986, 120-142 m, 2(AM W201623), 6.7 cm long; Townsville, 17°53.7'S 146°51.2'E, 21 Jan. 1985 (NTM W4300), 7 cm long.

Description. HOLOTYPE. Body ovate, rounded anteriorly, with tapering caudal region, 7.1 cm long, 4 cm wide, 43 segments.

Dorsum covered in fine, pale brown felt in alcohol, with some fine sediment entrapped in felt. Iridescent lateral fringe, reddish green in alcohol, extending well beyond neurosetae, along entire length of body (Fig.12). Some dark brown stouter notosetae. Ventral surface, cream coloured, tough, slightly areolated, covered with small flattened papillae.

Prostomium, small, ovoid, with 2 pairs of almost contiguous, faint grey eye spots. Pair of prominent, free flaps, arising from indented posterolaterally margin of prostomium. Median antenna reduced to a small, spherical papilla. Palps extending to segment 7, short basal palpophores, margins finely papillated. Facial tubercle 2 times length of prostomium, surface finely crenulated, inflated (Fig.13a).

Elytra 15 pairs, with firm stout attachments on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. First pair, smooth, opaque, ovoid, attached by thickened elytrophore centrolaterally. Subsequent elytra (based upon dissected paratype), increasing in size to middle of body, then decreasing in size posteriorly. Elytra rounded, with elytrophore attachments on lateral margin. Posterior 2 pairs elongated. Elytrophore on terminal pair attached anterolaterally, all elytra with a few submarginal micropapillae (Fig.13c-f).

Proboscis (dissected), thick, muscular, without jaws, ribbed muscular walls around opening.

First or tentacular segment with elongated, uniramous parapodia, projecting anteriorly and laterally to

Fig.12. *Aphrodita kulmaris* n.sp. (NMV F57187): dorsal view, whole animal.

prostomium, enlarged distally, forming small rounded lobe with aciculae and several radiating bundles of notosetae, globular flattened papillae on ventral surface. Two pairs of tentacular cirri with cylindrical tentaculophores. Dorsal and ventral tentacular cirri similar in length and shape, holotype missing 1 tentacular cirrus (Fig.13a).

Following segments with biramous parapodia. Second neuropodia, stout, rectangular, trilobed, consisting of 3 descending tiers, dorsoventrally, ridged epithelium with scattered flattened papillae. Neurosetae stout, darkly chitinised emergent from each lobe, progressively thicker dorsoventrally, upper tier with 1-2 neurosetae with extended smooth tips, middle tier with 3-4 neurosetae with extended tips, lower tier with many (100+) bipinnate neurosetae (Fig.14a). Aciculum, pale yellow, blunt-tipped, emergent between dorsal and ventral lobe. Ventral cirri, elongated, pointed, extending to just beyond tip of neuropodia. Notopodia squat, rectangular, on anterior face of neuropodia, without notosetae.

Third segment with parapodia and setae similar to those on segment 2, except slightly larger.

Following parapodia biramous (Fig.13b). Neuropodia with 3 tiers of golden brown neurosetae, many with pilose tips. Lower tier with 14-17 neurosetae (Fig.14b,e,h), middle tier with 5-9 neurosetae (Fig.14c,f,i), upper tier with 2-3 thicker, stouter, darker neurosetae (Fig.14d,g,j). Some neurosetae from anterior and posterior segments with extended tips, no pilose tips (Fig.14b-d,h). Notopodium with 2 fascicles of 10 or more golden brown spinous notosetae, entangled in numerous iridescent fine capillaries forming lateral fringe and dorsal felt. Notosetae smooth or with very fine tubercles (Fig.14k), some tips covered with a gelatinous sheath (Fig.14l), aligned laterally along body. Dorsal cirri long, slender, between three-quarters to as long as fringe of notosetal capillaries.

Variation. Additional material examined ranges from 1.8-10 cm long, 0.8-4.6 cm wide.with segments 38-46. Palps extending to segment 5-7. Facial tubercle varies from 1-2 times as long as prostomium. Median antenna in all material examined covered with small spherical papilla, no evidence of a style having ever been present.

In Table 4, the numbers of neurosetae present in each tier of segments 4, 15 and 25 are given for three size classes. The number of neurosetae in the upper tier is constant along the body and over the size range studied. In contrast the lower and middle tiers have higher numbers of neurosetae present on segment 15 than on

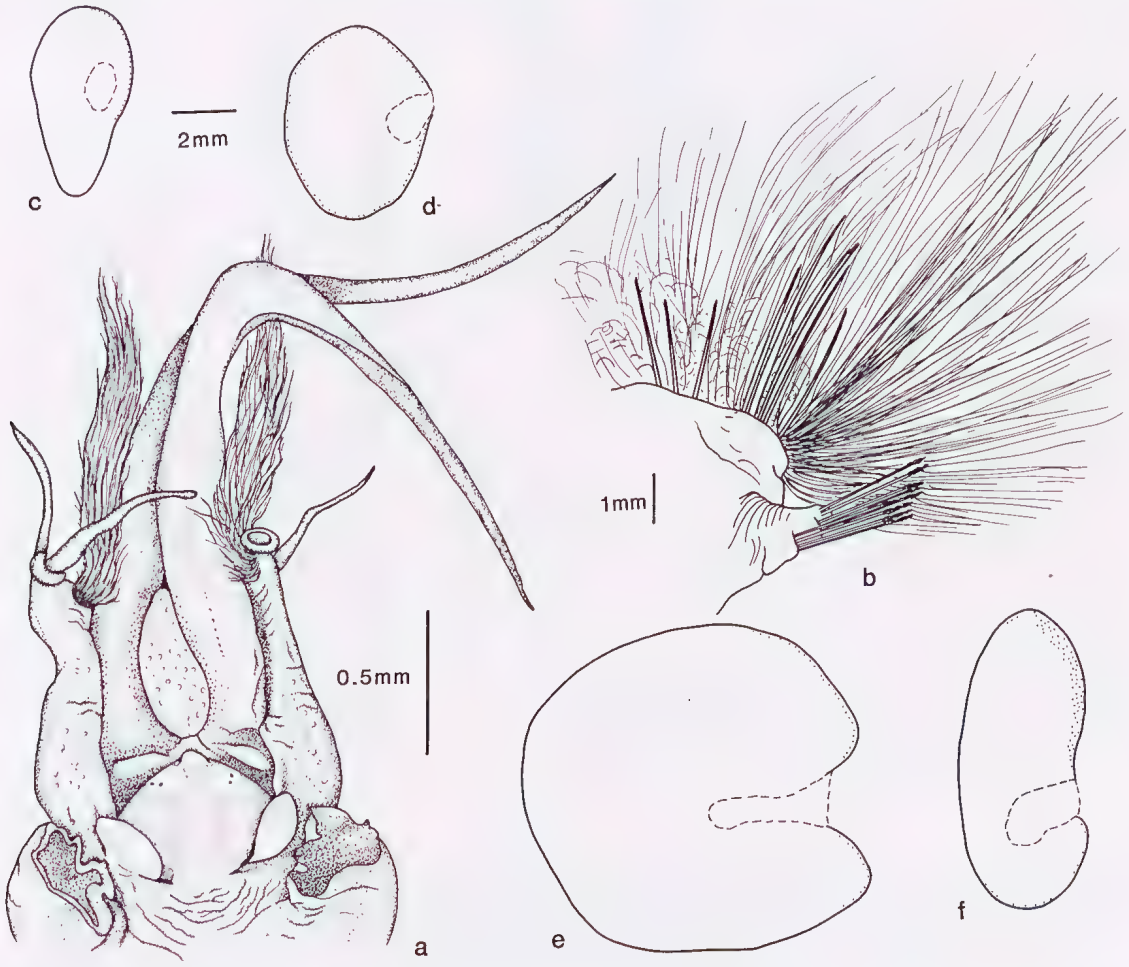

Fig.13. *Aphrodita kulmaris* n.sp. (AM W201623): a, dorsal view of prostomium and first segment; b, parapodium from segment 15; c, (AM W7959) first elytron; d, third elytron; e, eighth elytron; f, 14th elytron.

segment 4 or 25 regardless of size, however there is no clear pattern of setal numbers increasing in these tiers with increasing size and presumably age.

Remarks. *Aphrodita kulmaris* n.sp. can be distinguished from all other species of *Aphrodita* recorded from the Indo-Pacific by a small knob-shaped median antenna, a facial tubercle one to two times the length of the prostomium, stout, golden brown notosetae, a long iridescent reddish-brown lateral fringe and pilose tipped neurosetae (see Table 1). The species occurs in eastern and western Australian waters and these above characters clearly distinguish it from other species of *Aphrodita*, *A. australis*, *A. malkaris* n.sp. and *A. talpa* which also occur in these waters.

Habitat. Some individuals with sand and shell fragments within their felt and others were covered in mud, and they were dredged at depths of 9 to 146 m.

Etymology. The specific name is from an aboriginal word *Kulmaris* which means a shield and this species has the body of a shield.

Distribution. Australia (Long Reef, WA, 13°50'S 125°00'E, to Flinders Island, Qld, 14°09'S 144°04'E, Fig.59B).

Aphrodita limosa (Horst)

Figs 15a,b, 60, Table 1

Aphroditella limosa Horst, 1916b: 68.–Horst, 1917: 49, pl.XI figs 4-7.

Type material examined. HOLOTYPE: Indonesian Archipelago Stn 178: north of Ceram, 2°40'S 128°37.5'E, 835 m (ZMA V.Pol 71), 2.7 cm long, 1.8 cm wide, 36 segments.

Description. Body ovate, rounded anteriorly, tapering caudal region forming a tail, 2.7 cm long, 1.8 cm wide, 36 segments.

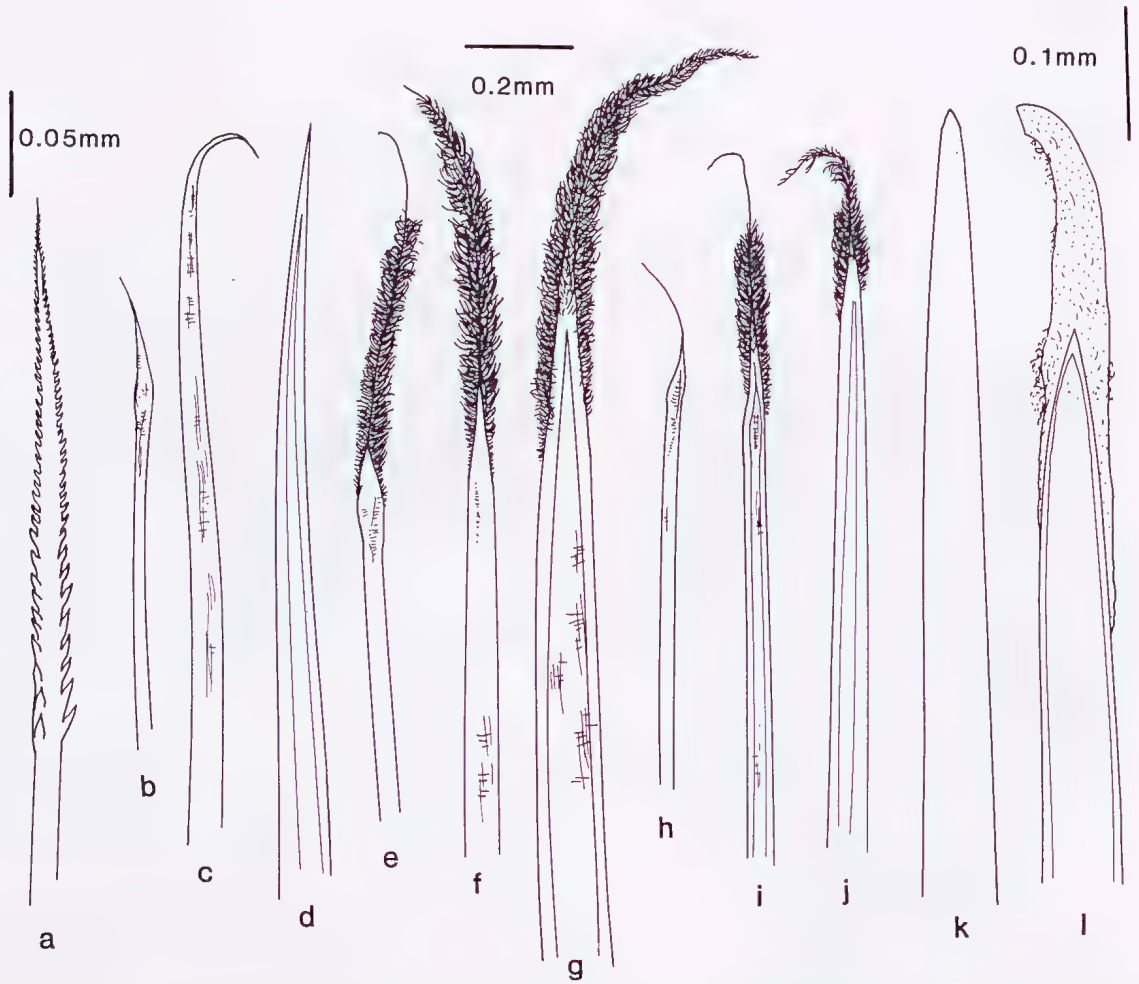

Fig.14. *Aphrodita kulmaris* n.sp. Holotype (NMV F57193): a, bipinnate neuroseta from segment 3; b, neuroseta from lower tier segment 4; c, neuroseta from middle tier segment 4; d, neuroseta from upper tier segment 4; e, neuroseta from lower tier segment 15; f, neuroseta from middle tier segment 15; g, neuroseta from upper tier segment 15; h, neuroseta from lower tier segment 25; i, neuroseta from middle tier segment 25; j, neuroseta from upper tier segment 25, k, notoseta from middle segment; l, tip of notoseta from middle segment.

Dorsum tan coloured in alcohol, covered in thick sand entrapped felt. Notosetae entangled amongst felt, fringe short, inconspicuous. Ventral surface tan coloured, densely papillated.

Prostomium oval, with pair of large, raised, hemispherical ocular areas, without pigment. Median antenna with short ceratophore, style thin, tapering, three-quarters length of prostomium. Palps extending to segment 7 with large basal palpophores, stout, tapering, finely papillated. Facial tubercle, length of prostomium, thin, covered in rounded papillae.

Elytra 17 pairs, attached to elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 27, 29, 32 and 35. Elytra opaque, covered with scattered micropapillae, first pair missing, remaining large, rounded, with elytrophore attachments on lateral margin, posterior pairs elongated with elytrophores attached anteriolaterally.

First or tentacular segment with elongated uniramous parapodia, projecting anteriorly and laterally to prostomium, with aciculae and tuft of pale yellow, capillary setae radiating from medial to posterior edge. Two pairs of tentacular cirri, with cylindrical tentaculophores, styles tapering with slender tips. Dorsal and ventral cirri subequal in length 2 times length of prostomium.

Following segments with biramous parapodia. Second and third neuropodia with 3 tiers of neurosetae: upper tier with 2, middle tier with 2-3, thick, golden brown, unidentate neurosetae with slightly curved tips, lower tier with tuft of many (50+), golden yellow, bipinnate neurosetae (Fig.15a). Buccal cirri slender with papillated cirrophore, extending past distal tip of neuropodia.

Remaining neuropodia cylindrical with 3 tiers of long, thin, golden brown neurosetae with slightly curved tips and plumose edge; upper tier with 2 thicker, darker neurosetae (Horst, 1917: pl.XI figs 5,6), middle tier with 3-4 neurosetae, lower tier with 6 neurosetae. Ventral cirri slender, tapering, extending to distal margins of neuropodia. Notopodia with tuft of short, faintly iridescent, mud-covered, capillary notosetae on ventral surface forming short, inconspicuous, lateral fringe. Dorsal surface of notopodia with fan of about 20 long, golden brown, notosetae, varying in thickness. Notosetae with bases smooth, distal one-third with fine tubercles and hairs, tapering to hooked tips (Fig.15b). Cylindrical cirrophores on posterior edge of notopodia, styles missing.

Fig.15. *Aphrodita limosa* (ZMA V.Pol 71): a, bipinnate neuroseta from segment 3; b, notoseta from middle segment.

Remarks. We have expanded Horst's (1916b, 1917) description of the species to include more details about the number and type of setae present. As this species is known only from the holotype and therefore we did not dissect the elytrae.

The reasons for referring this species to *Aphrodita* are given in the Remarks section of *A. decipiens*.

Aphrodita limosa which is known only from the holotype is characterised by the presence of relatively few neurosetae, short, mud-covered lateral fringe, a facial tubercle slightly longer than the prostomium, and smooth slightly curved tipped notosetae embedded in the felt (see Table 1).

Habitat. Trawled at a depth of 835 m.

Distribution. Indonesian Archipelago (Fig.60).

Aphrodita malayana (Horst)

Figs 16, 60, Table 1

Aphroditella malayana Horst, 1916b: 65-66.–Horst, 1917: 48-49, pl.XI figs 1-3.

Type material examined. LECTOTYPE: Indonesian Archipelago Stn 161: east off Kofiau Island, 1°10.5'S 130°09'E, 798 m (ZMA V.Pol 72.1), 3.7 cm long, 2.7 cm wide, 38 segments. PARALECTOTYPE: Indonesian Archipelago Stn 161: east off Kofiau Island, 1°10.5'S 130°09'E, 798 m (ZMA V.Pol 72.2), 3.5 cm long, 2 cm wide, 32 segments.

Description. Body ovate, rounded anteriorly, tapering caudal region forming a tail, 3.5-3.7 cm long, 2-2.7 cm wide, 32-38 segments.

Dorsal felt cream coloured in alcohol with some sand entrapped, setae long, red brown. Ventral surface tan coloured, densely covered with spherical papillae.

Prostomium rounded with raised hemispherical ocular area, without pigment. Median antenna, slender, just longer than prostomium. Palps with large basal palpophores one-third length of prostomium, extending to segment 6, margins finely papillated. Facial tubercle covered with small spherical papillae, length of prostomium.

First or tentacular segment with elongated, uniramous parapodia, projecting anteriorly and laterally to prostomium, slightly enlarged distally, forming rounded lobe, with tuft of golden yellow, mud-covered setae, equal in length to tentacular cirri, setae emerging radially from distal margins of lobe from inner to posterior edge. Two pairs of tentacular cirri, with cylindrical tentaculophores, styles, long, tapering. Dorsal pair of tentacular cirri one and one-quarter times length of prostomium, ventral pair of cirri three-quarters length dorsal pair.

Following segments with biramous parapodia. Second and third neuropodia with 2 tiers of neurosetae, upper tier with 2-3 dark red brown neurosetae with tips slightly curved, lower tier with tuft of about 100 golden yellow, bipinnate neurosetae (Fig.16a). Ventral cirri, slender, tapering, with cylindrical, papillated cirrophores arising from base of neuropodia, extending beyond tip of neuropodia, except ventral cirri of segment 3, arising from middle of neuropodia.

Remaining neuropodia with neurosetae long, thick, dark red brown, with slightly curved tips and plumose edges (Horst, 1917: pl.XI fig.3). Neurosetae in 3 tiers: upper tier with 2 neurosetae, middle tier with 3 neurosetae, lower tier with 3 neurosetae.

Notopodia with tuft of 15 or more, long dark red brown, thick notosetal spines on dorsal surface, pointing posterodorsally. Notosetae with finely tuberculated shafts anteriorly, shafts thicker, smooth posteriorly (Fig.16b). Lower surface of notopodia with tuft of short, faintly iridescent, mud-covered capillary notosetae, not forming lateral fringe. Dorsal cirri one and one-quarter length of stout notosetae, blunt tipped, entangled amongst felt.

Remarks. We have expanded Horst's (1916b, 1917) description of *A. malayana*, however the two specimens both lack eye pigment, although possessing raised ocular areas. In Horst's description he stresses the position of the two pairs of eyes which he regards as being different to the other species he described. The unpigmented raised ocular areas are located in a similar position to the other species described by Horst. The species is characterised by its lack of a lateral fringe, low number of neurosetae, long stout dark brown notosetae and a slender median antenna which is equal to the length of prostomium (see Table 1). The species is only known from these two type specimens.

For comments regarding the synonymising of

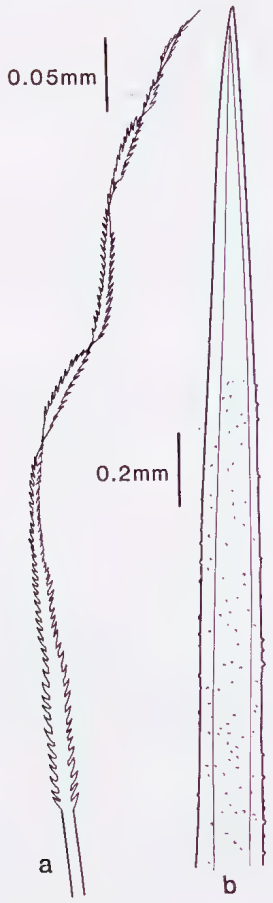

Fig.16. *Aphrodita malayana* (ZMA V.Pol 72.1): a, bipinnate neuroseta from segment 3; b, notoseta from middle segment.

Fig.17. *Aphrodita malkaris* n.sp. Holotype (WAM 88-89): dorsal view, whole animal.

Aphroditella with *Aphrodita*, see the Remarks section of *A. decipiens*.

Habitat. Trawled at a depth of 798 m.

Distribution. Indonesian Archipelago (Fig.60).

***Aphrodita malkaris* n.sp.**

Figs 17, 18a-f, 19a-k, 59B, Table 1

Type material examined. HOLOTYPE: Australia: Western Australia: Rowley Shoals, 16°58'S 120°07'E, 20 Aug. 1983, 428-432 m (WAM 88-89), 3 cm long, 2 cm wide, 35 segments.

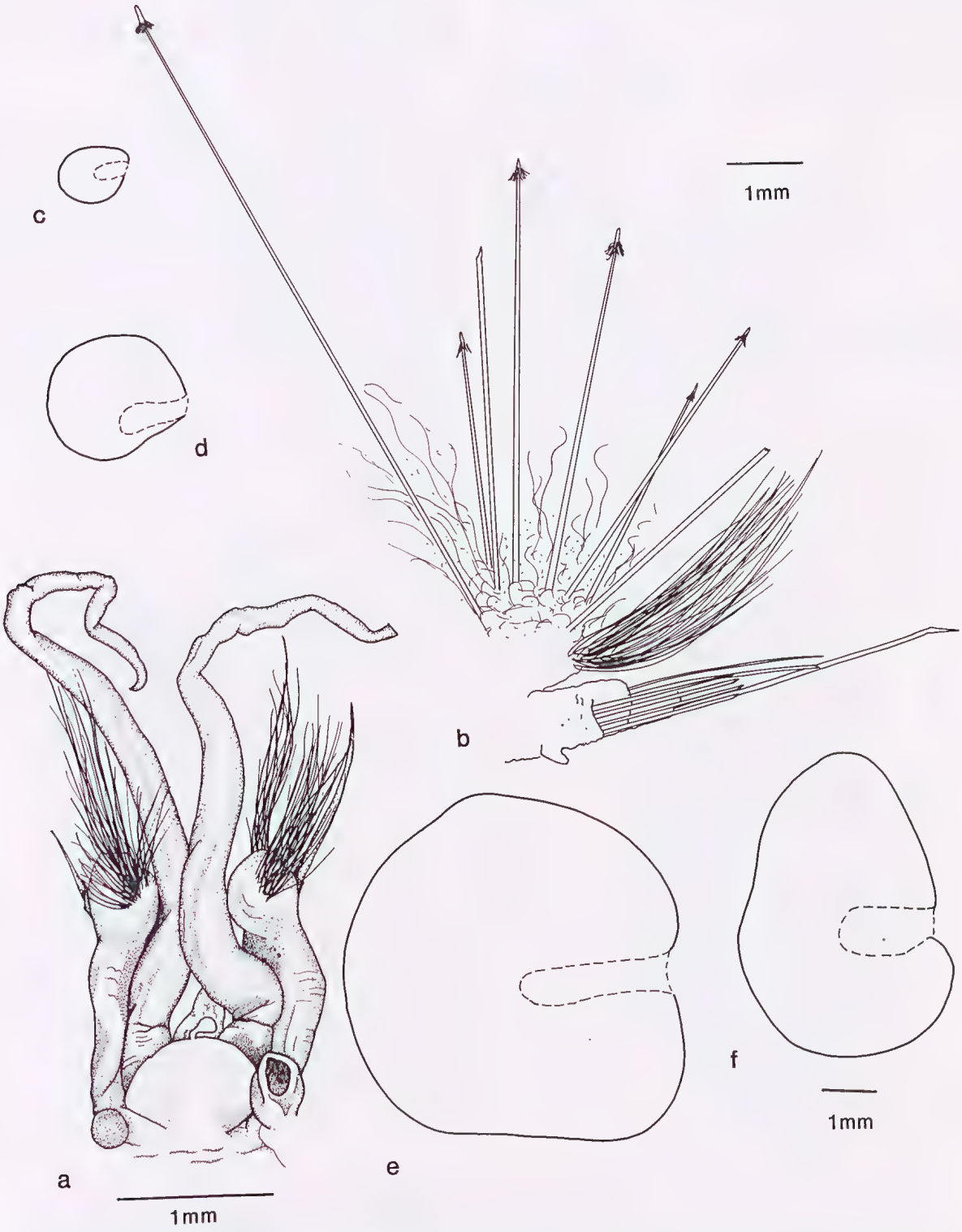

Fig.18. *Aphrodita malkaris* n.sp. Holotype (WAM 88-89): a, dorsal view of prostomium and first segment; b, parapodium from segment 15; c, Paratype (AM W20284) first elytron; d, third elytron; e, eighth elytron; f, 14th elytron.

PARATYPE: Western Australia: Rowley Shoals, 16°58'S 120°07'E, 20 Aug. 1983, 428-432 m (AM W20284), 2.7 cm long, 1.5 cm wide, 33 segments.

Description. Body ovate, 3.0 cm long, 2.0 cm wide, 35 segments.

Dorsal felt creamy grey in alcohol, setae long, red brown (Fig.17). Ventral surface covered with small, spherical papillae.

Prostomium rounded with raised hemispherical ocular area, without pigment. Median antenna, bulbous, one-third length of prostomium. Palps extending to segment 7, margins smooth. Facial tubercle covered with small spherical papillae, just shorter than prostomium (Fig.18a).

Elytra 15 pairs attached by elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. First pair of elytra rounded with elytrophore attached laterally. Remaining elytra squarish with rounded edges, increasing in size to middle of body, then decreasing in size posteriorly, elytrophores attached laterally. Posterior elytra ovoid with elytrophore attached anteriolaterally. All elytra smooth (Fig.18c-f).

First or tentacular segment with elongated, uniramous parapodia, covered with small spherical papillae, projecting anteriorly and laterally to prostomium, enlarged distally, forming rounded lobe, with tuft of golden yellow, mud-covered setae, equal in length to tentacular cirri, setae emerging radially from distal margins of lobe. Inner edge of parapodia with tuft of fine capillary setae. Two pairs of tentacular cirri, with cylindrical tentaculophores, styles, short, tapering. Dorsal pair of tentacular cirri 2 times length of prostomium, ventral pair of cirri just shorter than dorsal pair (Fig.18a).

Following segments with biramous parapodia (Fig.18b). Second and third neuropodia with 2 tiers of neurosetae, upper tier with 2 golden brown neurosetae with tips slightly curved, lower tier with tuft of many (100+) golden yellow bipinnate neurosetae (Fig.19a). Ventral cirri, slender, tapering, with cylindrical cirrophores arising from base of neuropodia, extending beyond tip of neuropodia, except ventral cirri of segment 3, arising from middle of neuropodia.

Remaining neuropodia with neurosetae long, thick, golden brown, with slightly curved tips, some with 1-2 small extra teeth, some smooth and some with short plumose edges. Neurosetae in 3 tiers: upper tier with

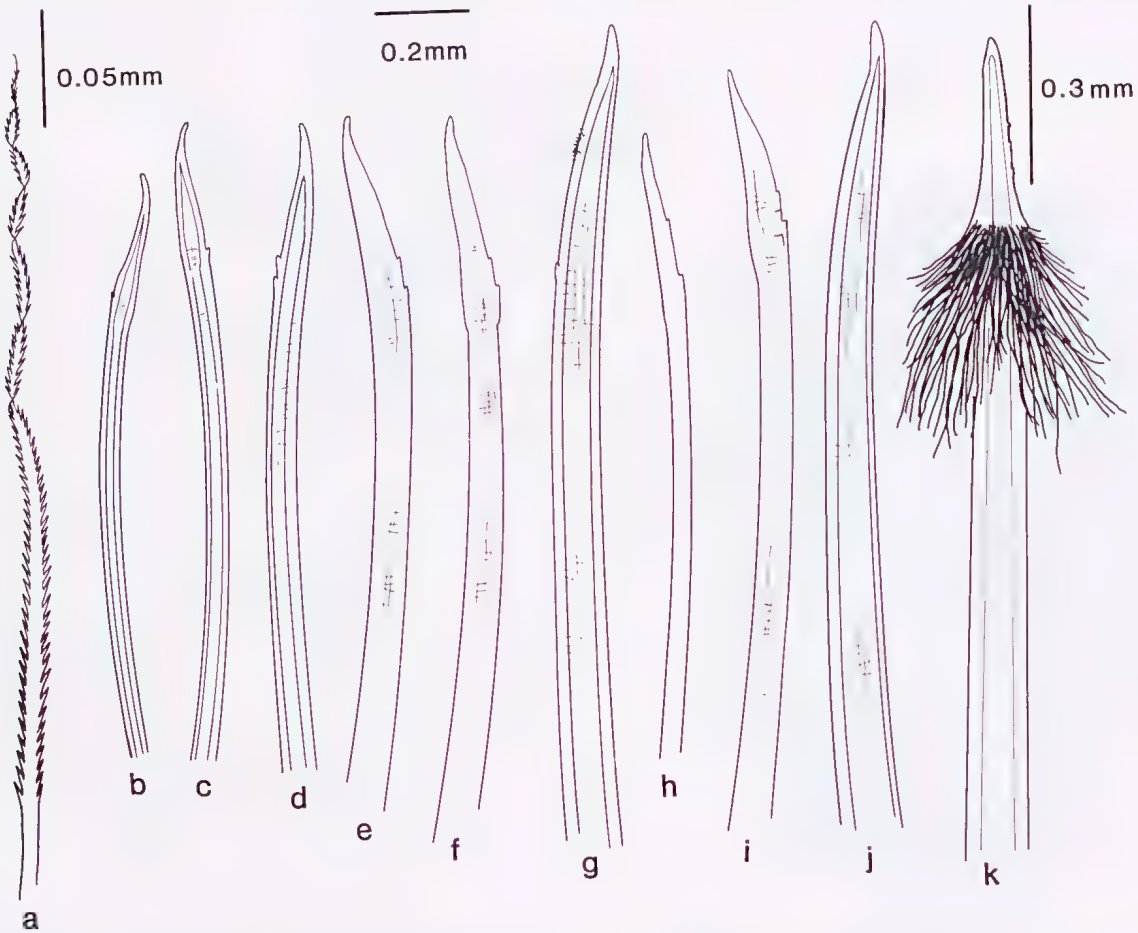

Fig.19. *Aphrodita malkaris* n.sp. Paratype (AM W20284): a, bipinnate neuroseta from segment 3; b, neuroseta from lower tier segment 4; c, neuroseta from middle tier segment 4; d, neuroseta from upper tier segment 4; e, neuroseta from lower tier segment 15; f, neuroseta from middle tier segment 15; g, neuroseta from upper tier segment 15; h, neuroseta from lower tier segment 25; i, neuroseta from middle tier segment 25; j, neuroseta from upper tier segment 25; k, tip of notoseta from middle segment.

2 neurosetae (Fig.19d,g,j), middle tier with 4 neurosetae (Fig.19c,f,i), lower tier with 6-7 neurosetae (Fig.19b,e,h).

Notopodia with tuft of 15-20, long golden brown notosetal spines on dorsal surface. Notosetae with smooth, finely striated shafts, with triangular shaped tips with numerous fine spines radiating from base of expansion (Fig.19k). Notosetae straight, fan posteriorly across dorsum, covering three-quarters of dorsum. Lower surface of notopodia with tuft of short, faintly iridescent, mud-covered capillary notosetae, not forming lateral fringe.

Variation. Additional material ranging from 2.7-3.0 cm long, 1.5-2.0 cm wide, with 33-35 segments.

Remarks. *Aphrodita malkaris* n.sp. can be distinguished from all other species of *Aphrodita*, recorded from the Indo-Pacific, by a bulbous median antenna which is about a third the length of the prostomium, long, triangular-tipped notosetae, short faintly iridescent lateral fringe, and its relatively low numbers of body segments (see Table 1). The species is currently known only from Western Australia, and these characters clearly distinguish it from other species of *Aphrodita*, *A. kulmaris* n.sp., *A. australis* and *A. talpa* which occur in these waters.

Habitat. Trawled from sandy substrates at depths of 428-432 m.

Etymology. The specific name is from an aboriginal word *Malkaris* which means a shield, and this species has the body form of a shield.

Distribution. Australia (Rowley Shoals, WA, 16°58'S 120°07'E, Fig.59B).

Aphrodita marombis n.sp.

Figs 20, 21a-e, 22a-k, 59C, Table 1

Type material examined. HOLOTYPE: Australia: Western Australia: Leighton Beach, 31°01'S 115°44'E, 22 June 1961, 15 m (WAM 31-75), 2.2 cm long, 1 cm wide, 36 segments. PARATYPES: South Australia: Reevesny Island, 34°33'S 136°17'E, 30 Jan. 1986 (SAM E2378), 5.1 cm long, 1.9 cm wide, 33 segments. New South Wales: Shell Harbour, 34°35'S 150°52'E, Apr. 1925 (AM W1597), 2.8 cm long, 1.2 cm wide, 32 segments; Shell Harbour, 34°35'S 150°52'E, Apr. 1925 (USNM 148661), 2.5 cm long, 1.3 cm wide, 35 segments; Shell Harbour, 34°35'S 150°52'E, Apr. 1925 (BMNH ZB 1990.22), 2.5 cm long, 1.5 cm wide, 35 segments.

Additional material examined. NEW SOUTH WALES: Port Stephens, 32°43'S 152°08'E (AM W20190), 1.3 cm long.

Description. Body oval 2.2 cm long, 1 cm wide, 36 segments.

Dorsum brown in alcohol, notosetae short, straight, golden yellow, covered with minute tubercles, not visible through felt (Fig.20). Ventral surface tan, covered with small rounded papillae.

Prostomium rounded with 2 large, raised, hemispherical ocular peduncles with 2 pairs of contiguous, grey/black eyes. Median antenna reduced to a small papilla, one-third length of prostomium, covered with small papillae. Facial tubercle inflated, covered with small round papillae, same length, or longer than prostomium. Palps extending to segment 4 or 5, margins finely papillated (Fig.21a).

Elytra 15 pairs attached by elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. First pair missing. Remaining elytra rounded, increasing in size to middle of body, then decreasing in size posteriorly, elytrophores attached laterally. Posterior elytra ovoid with elytrophores attached anterolaterally. All elytra smooth (Fig.21c-e).

First or tentacular segment with elongated, uniramous parapodia, projecting anteriorly to prostomium; with acicular and large node on inner, anterior edge. Tuft of stiff, golden yellow, mud-covered setae radiating around this node with 2 pairs of tentacular cirri, on anterior edge of parapodia, styles tapering with blunt tips. Dorsal and ventral cirri of same length, just longer than prostomium, tuft of fine, mud-covered setae on ventral surface, posterior to cirri (Fig.21a).

Following segments with biramous parapodia (Fig.21b). Second and third neuropodia cylindrical, finely

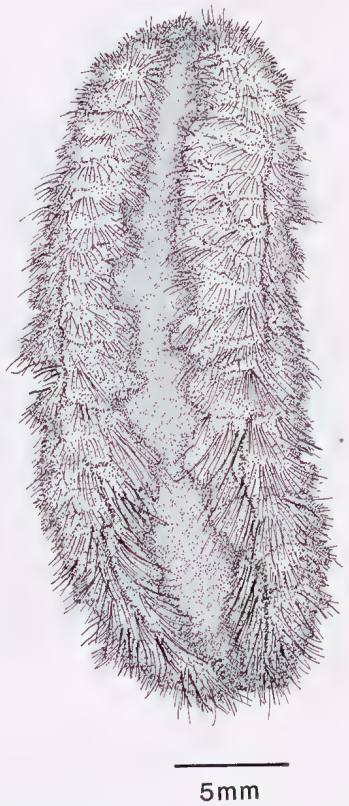

Fig.20. *Aphrodita marombis* n.sp. Paratype (AM W1597): dorsal view, whole animal.

papillated with 2 tiers of neurosetae; upper tier with 2 stout, golden brown neurosetae, with slightly curved tips, lower tier with tuft of many (20+) golden yellow, bipinnate neurosetae (Fig.22a). Ventral cirri with large, cylindrical, papillated cirrophore, emerging at base of neuropodia, styles with thick base and thinner blunt tip, extending past distal margins of neuropodia except ventral cirri on segment 3 emerging from middle of neuropodia.

Remaining neuropodia with 3 tiers of golden brown, stout neurosetae, with slightly curved tips, each with 2-3 neurosetae (Fig.22b-j). Some neurosetae of anterior and posterior segments with fine tubercles on curved margins (Fig.22e,h). Ventral cirri emerging from middle of neuropodia, extending between lower and middle tiers of neurosetae.

Notopodia with tuft of short, mud-covered, capillary notosetae, not forming fringe, emerging from ventral surface. Dorsal surface of notopodia with fan of about 30 straight, yellow, notosetae covered with many fine tubercles (Fig.22k), with tips just emerging from felt. Dorsal cirri tapering, with blunt tips, just longer than notosetae.

Variation. Additional material examined ranges from 1.3-5.1 cm long, 0.5-1.9 cm wide and 32-36 segments.

Remarks. *Aphrodita marombis* n.sp. can be distinguished from all other species of *Aphrodita*, recorded from the Indo-Pacific by its stout notosetae which are covered in small tubercles, stout mud-covered lateral fringe and its smooth neurosetae with slightly curved tips (see Table 1). The species is currently only known from southern Australia and these characters clearly distinguish it from other species of *Aphrodita*, *A. australis*, *A. bamarookis* n.sp., *A. goolmarris* n.sp. and *A. talpa* which also occur in these waters.

Habitat. Found amongst weed and rock with sand and shell fragments in their felt, and mud-covered notosetae. The only recorded depth of collecting was from 15 m.

Etymology. The specific name is from an aboriginal word *Marombis* which means a shield and refers to the shape of this new species.

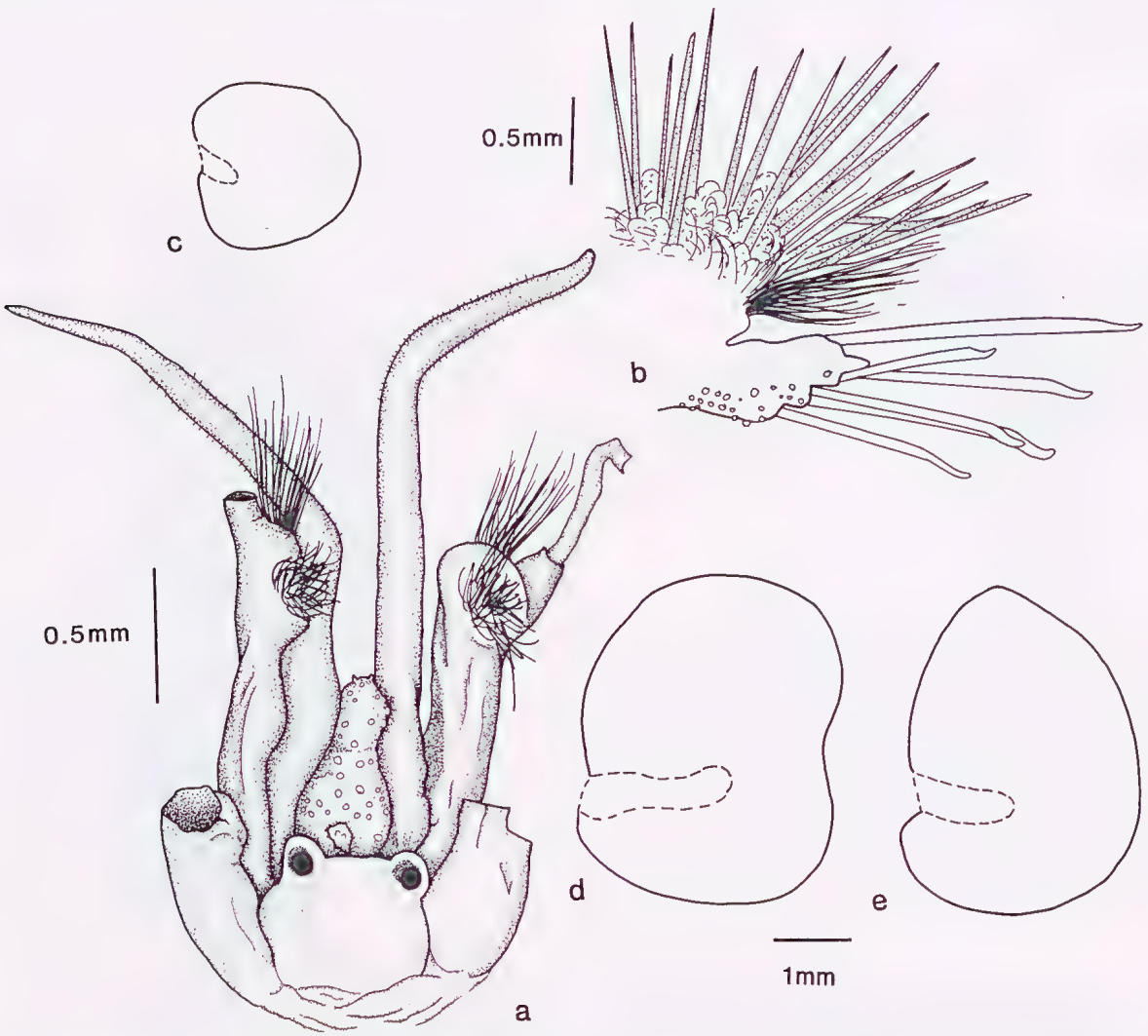

Fig.21. *Aphrodita marombis* n.sp. Paratype (AM W1597): a, dorsal view of prostomium and first segment; b, (AM W20190) parapodium from segment 17; c, third elytron; d, eighth elytron; e, 14th elytron.

Distribution. Australia (from Leighton Beach, WA, 31°01'S 115°44'E, to Port Stephens, NSW, 32°43'S 152°08'E, Fig.59C).

Aphrodita sibogae (Horst)

Fig.60, Table 1

Aphroditella sibogae Horst, 1916b: 66.–Horst, 1917: 50, pl.XI figs 8-10.

Material examined. None.

Remarks. This species is known only from a single specimen which was not available for examination. Horst provides a brief description of this species and this has been used in Table 1. The reasons for referring this species to *Aphrodita* are given in the Remarks section of *A. decipiens*.

Habitat. Trawled at a depth of 18 m.

Distribution. Indonesian Archipelago (between Loslos and Broken Islands, west of Salawatti, 1°01'S 130°52'E, Fig.60).

Aphrodita talpa Quatrefages

Figs 23a-f, 24a-k, 59C, Table 1

Aphrodite talpa Quatrefages,1866: 196-197, pl.VI figs 2-4.
Aphrodita talpa.–Fauvel, 1917: 167-168.–Fauvel, 1925: 140-144, fig.4.–Monro, 1936: 82-83, fig.3.

Material examined. WESTERN AUSTRALIA: Rottnest Island, 32°00'S 115°30'E, Mar. 1966 (WAM 53-75), 2 cm long. TASMANIA: Maria Island, 42°37'S 148°20'E, 9 Oct. 1984, 5(NMV F57203), 0.7-1.6 cm long; Falmouth, 41°32.9'S 145°35'E, 10 Oct. 1984 (NMV F57204), 1.7 cm long. NEW SOUTH WALES: Ulladulla, 35°21'S 150°29'E, 73-82 m (AM W20285), 1 cm long; Port Kembla, 34°20'S 151°18'E, 13 Dec. 1978, 161 m, 2(AM W20182), 1.1-1.2 cm long. QUEENSLAND: Shaw Island, 20°32.3.'S 149°01.4'E, 19 Nov. 1977, 27 m (AM W20181), 2.3 cm long; Cape York, 12°45.6'S 143°32.2'E, 28 Sept. 1979, 19.8 m (QM GH285), 4.5 cm long.

Additional material examined. HOLOTYPE of *Aphrodita*

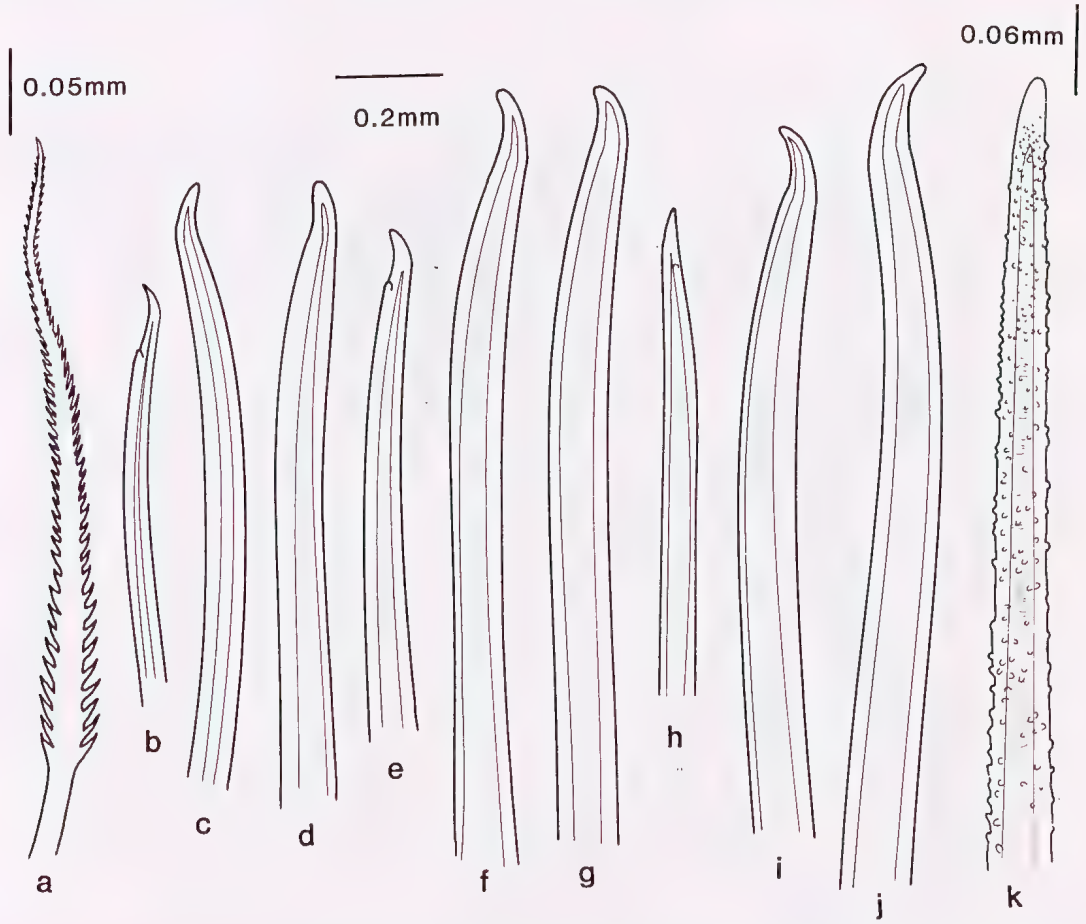

Fig.22. *Aphrodita marombis* n.sp. Paratype (AM W1597): a, bipinnate neuroseta from segment 3; b, neuroseta from lower tier segment 4; c, neuroseta from middle tier segment 4; d, neuroseta from upper tier segment 4; e, neuroseta from lower tier segment 15; f, neuroseta from middle tier segment 15; g, neuroseta from upper tier segment 15; h, neuroseta from lower tier segment 25; i, neuroseta from middle tier segment 25; j, neuroseta from upper tier segment 25; k, notoseta from middle segment.

armifera. USA: California: Monterey Bay, 36°45'N 122°00'W, 9 June 1904, 97-99 m, (USNM 16849).

Description. Body ovoid, with attenuated caudal region forming tail, 0.7-4.5 cm long, 0.4-2.2 cm wide, 31-38 segments.

Dorsum brown coloured in alcohol, thin felt covering elytra. Golden notosetae amongst felt. Ventral surface tan, covered with many small, spherical papillae.

Prostomium small, rounded, with 2 raised hemispherical ocular areas with 2 pairs small black eyes of same size. Median antenna elongate with slightly enlarged tip, similar length to prostomium. Palps extending to segment 3-5, palphophores less than one-quarter length of prostomium, margins smooth. Facial tubercle three-quarters length of prostomium, covered in small spherical papillae, partly hidden by palps dorsally (Fig.23a).

Elytra 15 pairs, with firm stout attachments to elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra opaque, first pair rounded with elytrophore attached centrally, following elytra large, rounded with elytrophores attached laterally, posterior elytra elongate with elytrophores attached anterolaterally. All elytra with some scattered micropapillae (Fig.23c-f).

First or tentacular segment with elongated, flattened, uniramous parapodia, with few scattered papillae. Inner, anterior edge of parapodia with tuft of fine, short, pale yellow, capillary setae, also tuft of fine, pale yellow setae on distal tip and ventral surface of parapodia, 2 pairs of cylindrical tentaculophores on upper edge of parapodia, tentacular cirri with slightly enlarged distal tips, dorsal and ventral pair same length, one-third length of palps (Fig.23a).

Following segments with biramous parapodia (Fig.23b). Second and 3rd neuropodia with 2 tiers of

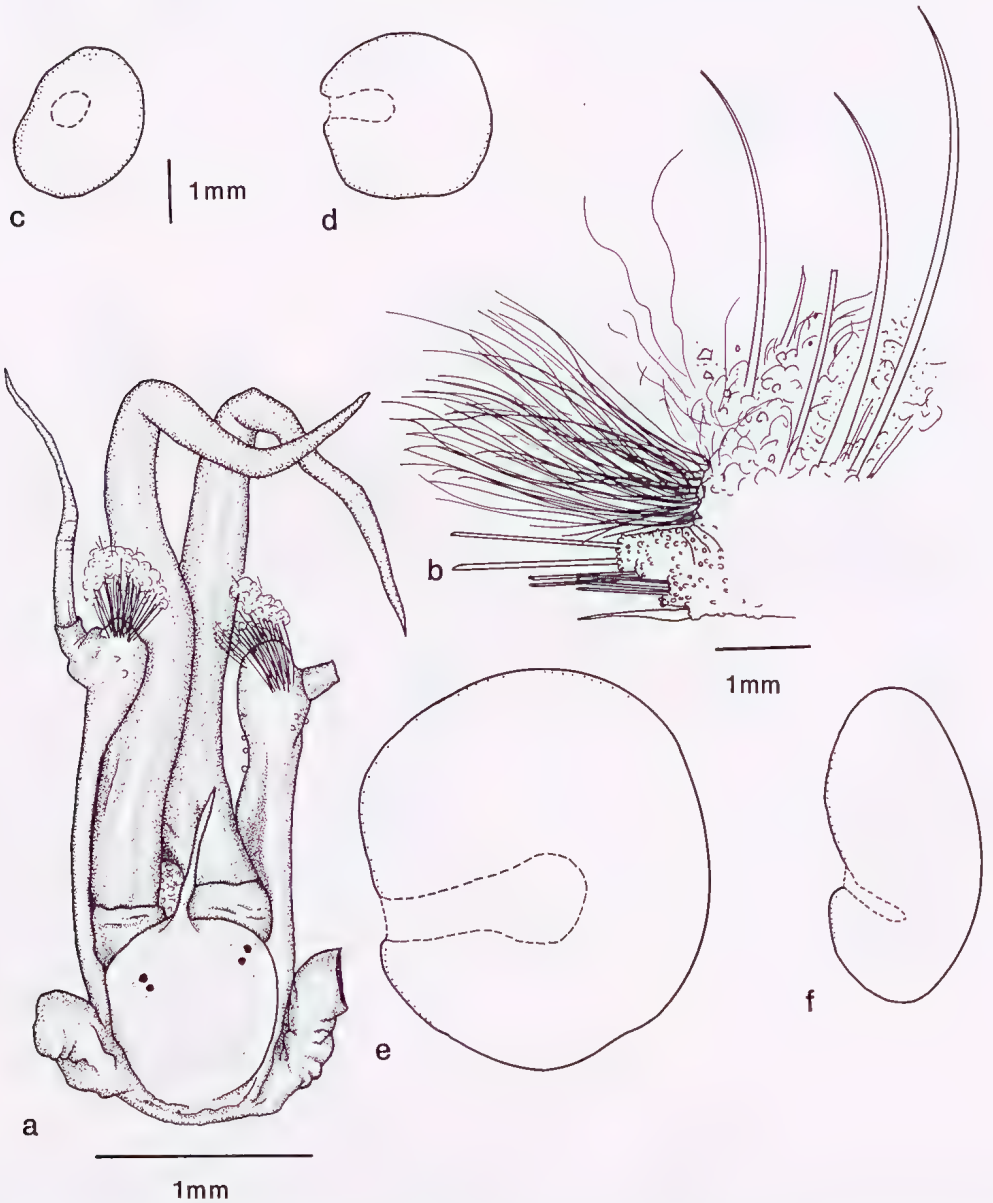

Fig.23. *Aphrodita talpa* (NMV F57203): a, dorsal view of prostomium and first segment; b, parapodium from segment 15; c, (AM W20181) first elytron; d, third elytron; e, eighth elytron; f, 12th elytron.

neurosetae: upper tier with 2 golden brown, unidentate neurosetae with slightly curved tips, lower tier with tuft of many (20+), golden yellow, bipinnate neurosetae (Fig.24a). Ventral cirri slender, tapering, arising on base of neuropodia with papillated cirrophores, not extending beyond distal tip of neuropodia.

Remaining neuropodia cylindrical, covered in rounded papillae (Fig.23b), with 3 tiers of golden brown neurosetae with slightly curved tips, with short plumose beard on inner side underneath curve (Fig.24g). Upper tier with 2 stouter, thicker, darker neurosetae (Fig.24d,g,j), middle tier with 3-5 neurosetae (Fig.24c,f,i), lower tier with 5-8 neurosetae (Fig.24b,e,h). Ventral cirri delicate, elongate, arising in middle of neuropodia, not extending beyond distal tip of neuropodia.

Notopodia stout, with tuft of faintly iridescent, mud-covered, capillary notosetae, not extending past neurosetae and not forming conspicuous lateral fringe. Notosetae golden brown, tapering to hooked tips, shafts smooth (Fig.24k) or finely tuberculated with fine hairs attached (Fig.24l) occurring in 2 fascicles: lateral one with greater than 10, short, straight notosetae which fan posteriorly, tips only emergent from felt; inner one with 5-8 notosetae, long, curving over dorsum and entangled amongst felt, covering three-quarters dorsum. Dorsal cirri blunt tipped, one-third length of longer notosetae.

Variation. Larger specimens with faint grey eye spots, or without pigment. Palps finely papillated, median antenna half length of prostomium.

Remarks. *Aphrodita talpa* was originally described by Quatrefages (1866) from New Zealand and subsequently recorded from Australia. Day & Hutchings (1979) indicated in their checklist, which was based entirely on the literature, that Fauvel's (1917) record of this species from South Australia, was not *A. talpa* Quatrefages. Fauvel (1925) in a partial review of the genus synonymised his material of *A. talpa* from South Australia with *A. armifera* Moore, 1910, a species occurring on the west coast of America. However, Fauvel (1925) clearly states on page 140 that he examined the type of *A. talpa* Quatrefages, and this closely resembled his material from South Australia. We therefore suggest that *A. talpa* Quatrefages does occur in Australia, based on Fauvel's (1925) description of his material from South Australia. However, we do not concur with his synonomising of *A. talpa* Quatrefages with *A. armifera* Moore, as the holotype of *A. armifera*

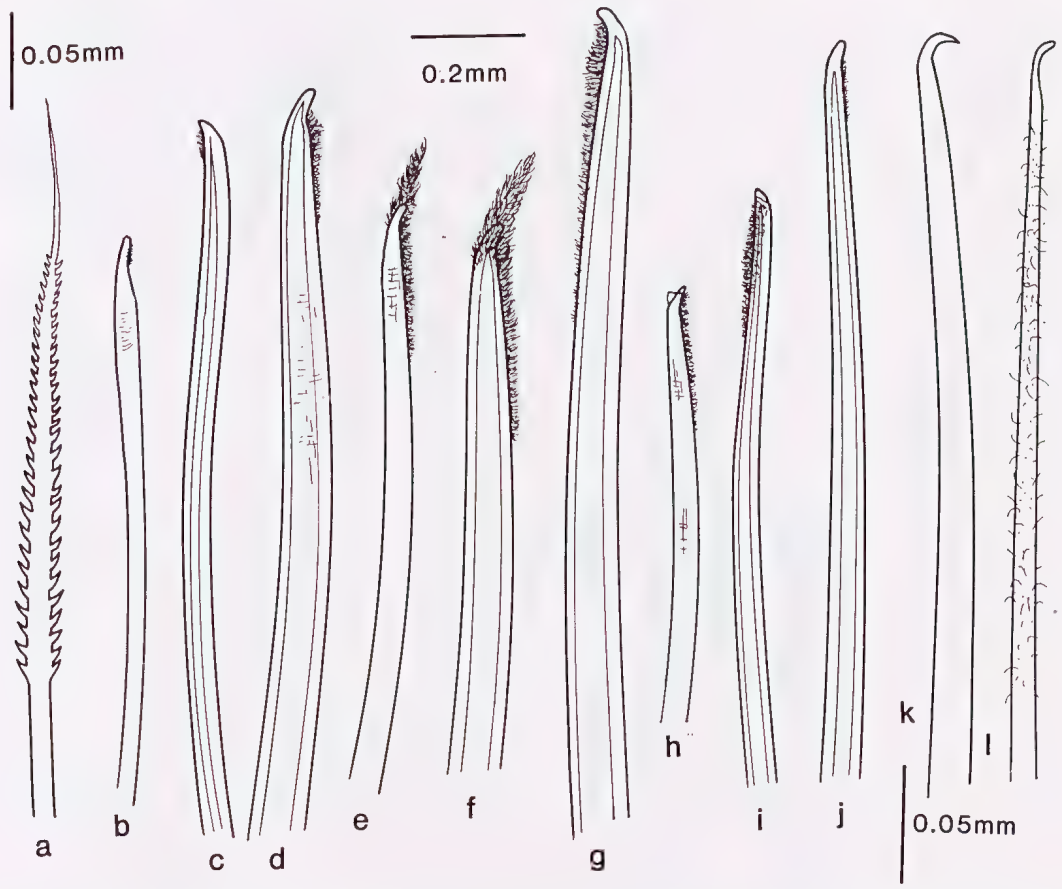

Fig.24. *Aphrodita talpa* (NMV F57203): a, bipinnate neuroseta from segment 3; b, neuroseta from lower tier segment 4; c, neuroseta from middle tier segment 4; d, neuroseta from upper tier segment 4; e, neuroseta from lower tier segment 15; f, neuroseta from middle tier segment 15; g, neuroseta from upper tier segment 15; h, neuroseta from lower tier segment 25; i, neuroseta from middle tier segment 25; j, neuroseta from upper tier segment 25; k, notoseta from middle segment; l, notoseta from middle segment.

(USNM 16849) was examined and clearly differs from *A. talpa*.

Other records of *A. talpa* from New Zealand by Ehlers, 1907; Benham, 1900; Augener, 1922 have not been verified by checking their material.

We have been unable to locate the type of *A. talpa* in the Museum D'Histoire Naturelle in Paris, and perhaps Fauvel did not return Quatrefages material after examination. Unfortunately Quatrefages gives only New Zealand as the type locality which makes obtaining representative material from the type locality and the designation of a neotype impossible. However, Fauvel's (1925) description of *A. talpa* is sufficiently detailed to enable us to identify a large amount of material as belonging to this species. Only if material of *Aphrodita* from New Zealand and none was available, was found

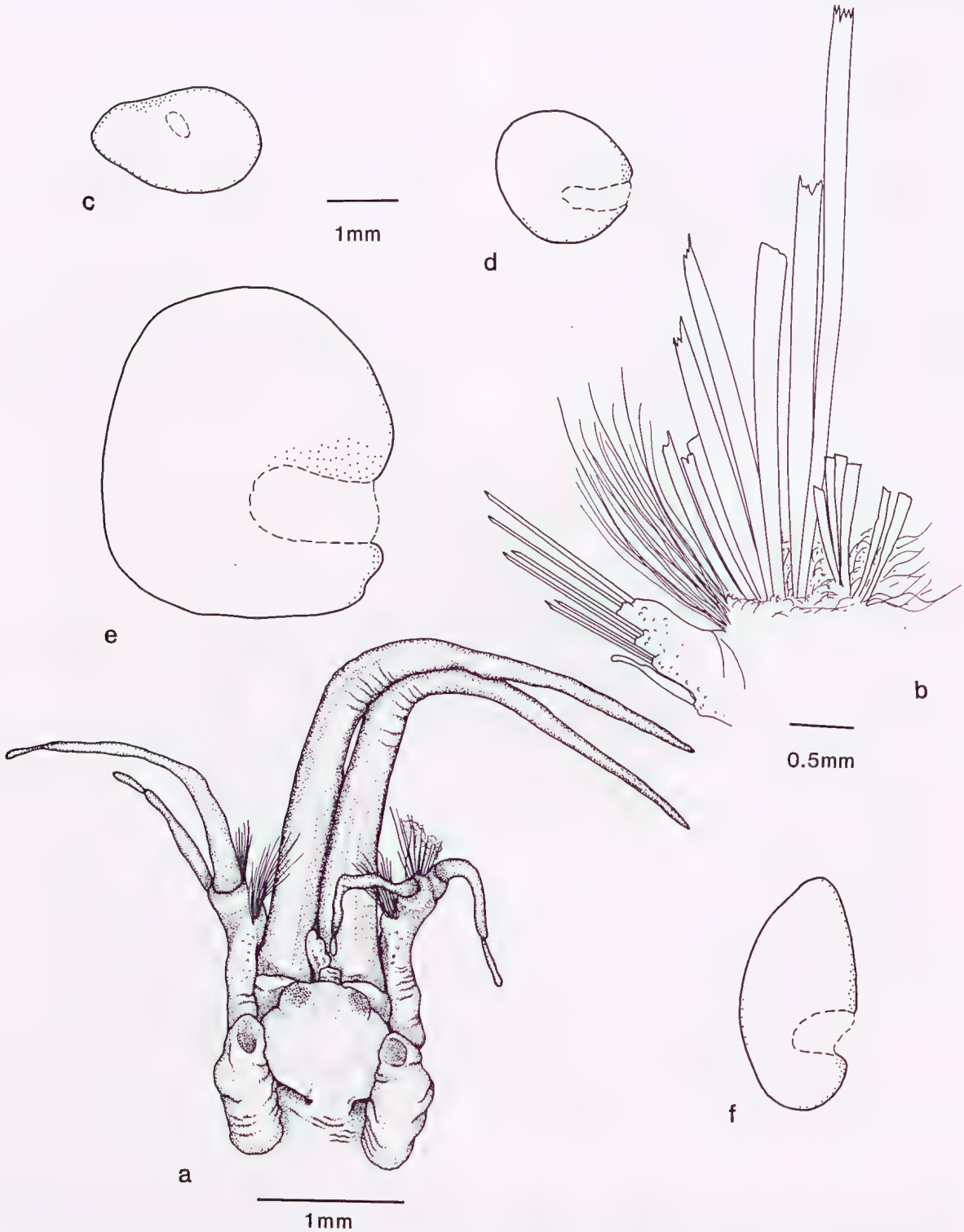

Fig.25. *Aphrodita terraereginae*. Holotype (AM G11245): a, dorsal view of prostomium and first segment; b, parapodium from segment 15; c, first elytron; d, third elytron; e, eighth elytron; f, 14th elytron.

to be different to our Australian material of *A. talpa*, would we erect a new species to include the material which we have referred to as *A. talpa* Quatrefages.

Aphrodita talpa is characterised by the following suite of characters, smooth palps, smooth notosetae entangled in the felt, a short faintly iridescent lateral fringe, and neurosetae with slightly curved tips and a plumose edge (see Table 1). This combination of characters distinguishes it from all other species of *Aphrodita* described from the Indo-Pacific.

We have recorded *A. talpa* from a wide area of Australian waters.

Habitat. Trawled at depths of 19.8 to 161 m.

Distribution. Australia (Rottnest Island, WA, 32°00'S 115°30'E, to Cape York, Qld, 12°45.6'S 143°32.2'E, Fig.59C). Japan, Kushiro* (Imajima, 1964); New Zealand (Quatrefages, 1866; Ehlers, 1907*; Benham, 1900*; Augener, 1922*).

Aphrodita terraereginae Haswell

Figs 25a-f, 26a-f, 59A, Table 1

Aphrodita terraereginae Haswell, 1883: 271.

Material examined. QUEENSLAND: Cape Flinders, 14°08'S 144°14'E, 6 m (AM G11245), 2.5 cm long.

Description. Body elongate, oval, 2.5 cm long, 1.1 cm wide, 40 segments.

Dorsum cream coloured in alcohol, covered in thin, fine felt with thick pale yellow paleal-like notosetae. Short inconspicuous, cream coloured lateral fringe. Ventral surface coloured cream, smooth, minutely papillated.

Prostomium rounded, 1 pair large grey, slightly raised eyes. Median antenna small, rod shaped (style missing). Palps with basal palphophores extending to segment 7, with tapering ventral palps, margins finely papillated. Facial tubercle one-third length of prostomium, thin, covered with small rounded papillae (Fig.25a).

Elytra, 15 pairs, firmly attached to elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra smooth, transparent, slightly iridescent, first pair ovoid with elytrophore attached centrally; second pair rounded, with elytrophores attached laterally, third pair rounded with elytrophores attached anteriolaterally. Following elytra up to segment 19 rounded with elytrophores attached laterally, remaining elytra oval, becoming more elongated towards caudal region with elytrophores attached anterolaterally. All elytra with a few sub-marginal micropapillae (Fig.25c-f).

First or tentacular segment with elongated uniramous parapodia, projecting anteriorly and laterally to prostomium. Two pairs of tentacular cirri on anterior end of parapodia, with cylindrical tentaculophores, styles tapering with clavate tips, dorsal and ventral tentacular cirri subequal, one-third length of palps. Tuft of fine capillary setae radiating around distal tip of parapodia, also small tuft of ventral setae.

Following segments with biramous parapodia (Fig.25b). Second and third neuropodia with 2 tiers of neurosetae: upper tier with 2-3 neurosetae (all broken), lower tier with tuft of many, golden yellow, bipinnate neurosetae (Fig.26a). Ventral cirri slender, clavate-tipped, 2 times length of neuropodia.

Remaining neuropodia cylindrical with 3 tiers of golden brown neurosetae with slightly curved tips; upper tier with 2 thicker, darker neurosetae (Fig.26d), middle tier with 3-4 neurosetae (Fig.26c), lower tier with 3-4 neurosetae (setae damaged). Some neurosetae of anterior segments with slightly curved tips and some fine hairs on curved margin (Fig.26d,e). Ventral cirri slender, clavate-tipped, extending just beyond distal margins of neuropodia. Notopodia with tuft of faintly iridescent, capillary notosetae covered in cream, calcareous mud on ventral surface forming short lateral fringe. Dorsal surface of notopodia with fan of 7 or more large, thick, smooth, pale yellow notosetae with most tips broken, covering entire dorsum, some posterior notosetae entire, with rounded tips (Fig.26f). Dorsal cirri clavate-tipped, one-third length of large notosetae.

Remarks. The species is known only from a single individual, and most of the notosetae are broken. Day & Hutchings (1979) indicated that the type was lost, however in the AM collection we discovered this single specimen labelled as the holotype of *A. terraereginae*,

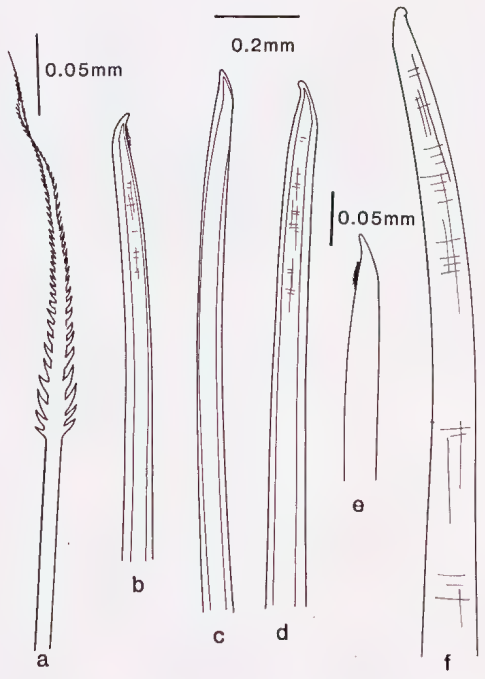

Fig.26. *Aphrodita terraereginae*. Holotype (AM G11245): a, bipinnate neuroseta from segment 3; b, neuroseta from upper tier segment 4; c, neuroseta from middle tier segment 15; d, neuroseta from upper tier segment 15; e, neuroseta from middle tier segment 25; f, tip of notoseta from posterior segment.

collected from the same locality and of a similar size to the individual described by Haswell. This specimen was registered in 1908, by McCulloch who was the Invertebrate curator at the Australian Museum at this time. It appears that Haswell who was Professor of Zoology at Sydney University did not designate a holotype and that McCulloch subsequently designated this specimen as the holotype. While it seems likely that it is the holotype of *A. terraereginae*, we cannot categorically state that it was the specimen examined by Haswell although it agrees with Haswell's description.

Aphrodita terraereginae is characterised by long, finely papillated palps, a small rod-shaped antenna, thick paleal-like smooth pale yellow notosetae, short faintly iridescent lateral fringe and neurosetae with slightly curved tips (see Table 1). This suite of characters clearly distinguishes it from all the other species of *Aphrodita* described from the Indo-Pacific.

Habitat. No habitat information available, found at a depth of 6 m.

Distribution. Australia (Cape Flinders, Qld, 14°08'S 144°14'E, Fig.59A).

Aphrogenia Kinberg

Aphrogenia Kinberg, 1856: 382.–Pettibone, 1966: 98.

Diagnosis. Aphroditids without well-developed dorsal felt covering elytra. Elytra 13-15 pairs, with scattered papillae. Prostomium with globular ocular lobes. Facial tubercle present. Notosetae all smooth, of 2 kinds: stout, smooth sabre-like, long, curved over dorsum and fine capillary setae. Neurosetae, dark, stout with basal spur. Neurosetae of anterior few segments with extra teeth, some bipinnate.

Type species. *Aphrogenia alba* Kinberg, 1856, by monotypy.

Remarks. The above definition of the genus is based upon Pettibone (1966), but we have expanded the definition to include the presence of globular ocular lobes, and a variable number of elytra. A generalised figure of *Aphrogenia* is given in Figure 27 together with the types of setae present.

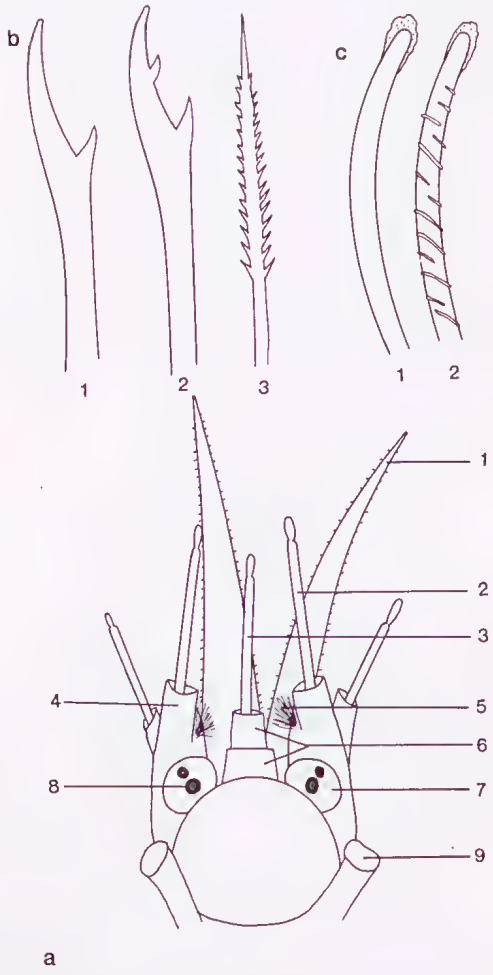

Fig.27. Generalised *Aphrogenia*. a: dorsal view of prostomium and first segment – 1, papillated palp; 2, tentacular cirrus; 3, median antenna; 4, tentaculophore; 5, setae; 6, 2-jointed ceratophore; 7, ommatophore; 8, eye; 9, elytrophore. b: neurosetal types – 1, bidentate; 2, bidentate with 1 extra tooth; 3, bipinnate. c: notosetal types – 1, sabre notoseta, smooth; 2, sabre notoseta, ridged.

Key to the Indo-Pacific Species of *Aphrogenia*

1. Sabre-like notosetae smooth (Fig.29e-g) 2

—— Sabre-like notosetae with ridges (Fig.31c) ..... *Aphrogenia villosa*

2. Elytrigerous notopodia with fan of about 9 sabre-like notosetae (Fig.29e-g) ..... *Aphrogenia margaritacea*

—— Elytrigerous notopodia with fan of 2-3 sabre-like notosetae, cirrigerous notopodia with black spot anteriorly ..... *Aphrogenia nigropunctata*

Aphrogenia margaritacea Augener

Figs 28a-f, 29a-g, 59D, Table 5

Aphrogenia margaritacea Augener, 1913: 93-96, fig.3, pl.II figs 1,2.

Material examined. WESTERN AUSTRALIA: Arthur Head, 32°03'S 115°44'E, 25 Dec. 1983, 6 m (AM W20228); Dunsborough, 33°36'S 115°06'E, 27 Dec. 1971, 16.5 m (AM W201443), 1 cm long. VICTORIA: Cribb Point, 38°21'S 145°13'E (NMV F57198), 1 cm long; Bass Strait, 39°28'S 148°48'E, 21 Nov. 1981, 84 m (NMV F57083), 1.5 cm long.

Description. Body oval, 0.4-1.5 cm long, 0.2-0.5 cm wide, 22-32 segments.

Dorsum yellow coloured in alcohol, elytra with pearl-like shine. Ventral surface cream coloured, covered with many rounded papillae.

Prostomium rounded with 2 large ocular lobes one-third length of prostomium, each with 2 pairs of black eyes. Median antenna with ceratophore 2-jointed just longer than prostomium; style longer than palps, 2-jointed with clavate process at tip. Facial tubercle, small, located below ceratophore visible only ventrally, covered with cylindrical papillae. Palps extending to segment 5, tapering with papillated margins (Fig.28a).

Elytra, 15 pairs, attached by elytrophores on segments

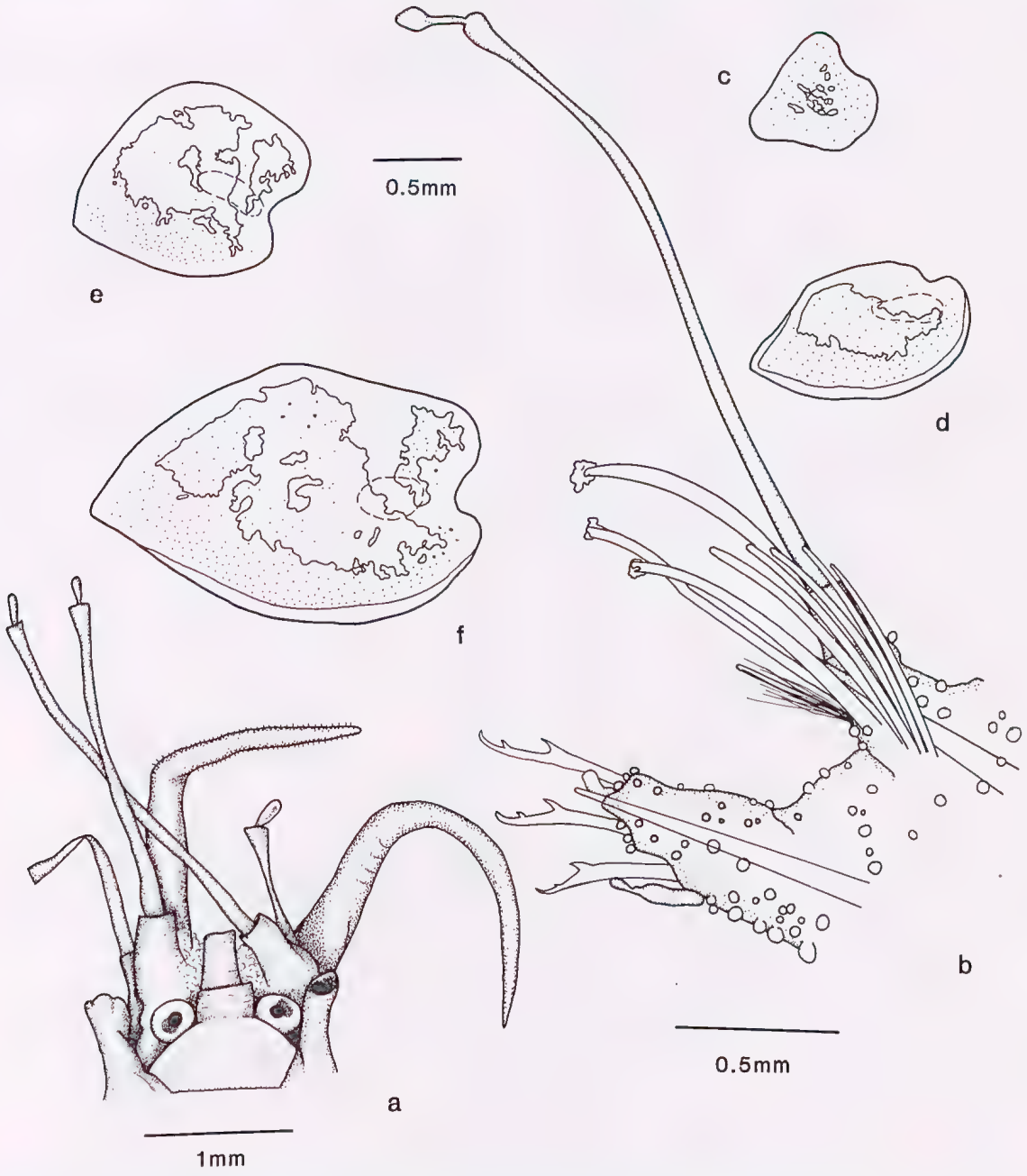

Fig.28. *Aphrogenia margaritacea* (NMV F57083): a, dorsal view of prostomium (median antenna missing) and first segment; b, posterior view of parapodium 16; c, (AM W201443) first elytron; d, third elytron; e, eighth elytron; f, 14th elytron.

2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra thin, transparent, opalescent, covered in scattered microtubercles, some with dark brown patches, first pair small, triangular with rounded edges, following elytra large, leaf-shaped with elytrophores attached laterally. All elytra covered with scattered micropapillae (Fig.28c-f).

First or tentacular segment with elongated, uniramous parapodia, projecting anteriorly to prostomium, above palps; with aciculae and large terminal asymmetrical lobe on anterior, inner edge, covered with many cylindrical papillae; short tuft of capillary setae emerging radially from distal margins of lobe, and 2 pairs of clavate-tipped cirri with large cylindrical tentaculophores, dorsal pair as long as palps, ventral pair three-quarters length of dorsal pair (Fig.28a).

Parapodia of segment 2 biramous, neuropodia cylindrical, covered with large, rounded papillae, 2 yellow bidentate neurosetae on outer end of neuropodia, between these neurosetae emerging small curved appendage, lower tuft of many (20+), yellow, bipinnate (Fig.29a) neurosetae. Ventral cirri with clavate tips emerging at base of neuropodia, extending to tuft of bipinnate neurosetae. Notopodia with tuft of fine, pale yellow notosetae emerging from, rounded, distal end.

Third segment similar to second except ventral cirri emerging just below bipinnate setae, and notopodia with sabre-like notosetae.

Following segments with biramous parapodia (Fig.28b). Neuropodia cylindrical, covered in large globular papillae, with 3-4 golden yellow neurosetae with slightly hooked tips, with basal spur and with or without distal tooth on curved margin (Fig.29b-d). Anterior and posterior neurosetae thinner, elongate. Ventral cirri, with clavate tips, emerging just below ventral setae and extending below distal margins of neuropodia.

Elytrigerous notopodia with fan of 9 or more, pale yellow, flattened, smooth, sabre-like notosetae with rounded mud-covered tips, arching over entire dorsum (Fig.29e-g); lower surface of notopodia with small tuft of fine, mud-covered, capillary notosetae.

Cirrigerous notopodia with cylindrical cirrophores on distal ends of notopodia with styles of dorsal cirri with clavate tips varying in length from one-half to one and one-half times length of sabre notosetae. Dorsal surface of notopodia with fan of about 9 thin, pale sabre notosetae arching over neuropodia; notosetae shorter than sabre notosetae of elytrigerous notopodia. Lower surface of notopodia with tuft of fine, mud-covered capillary notosetae.

Variation. Eye pigment missing from some specimens. One specimen with bright red opalescent elytra, and ventral side pale pink in alcohol.

Remarks. This expands the geographical distribution of the species which was previously known only from the type locality of Western Australia. This species which is characterised by the number of sabre-like notosetae in the fan-like arrangement on elytrigerous segments, which clearly distinguishes it from other Indo-Pacific species (Table 5).

Habitat. Found on limestone, and coral reefs, in shelly sand, one specimen found with spirorbid polychaetes attached to dorsum. Found in depths of 6-84 m.

Distribution. Australia (Arthur Head, WA, 32°03'S 115°44'E to Cribb Point, Vic., 38°21'S 145°13'E, Fig.59D).

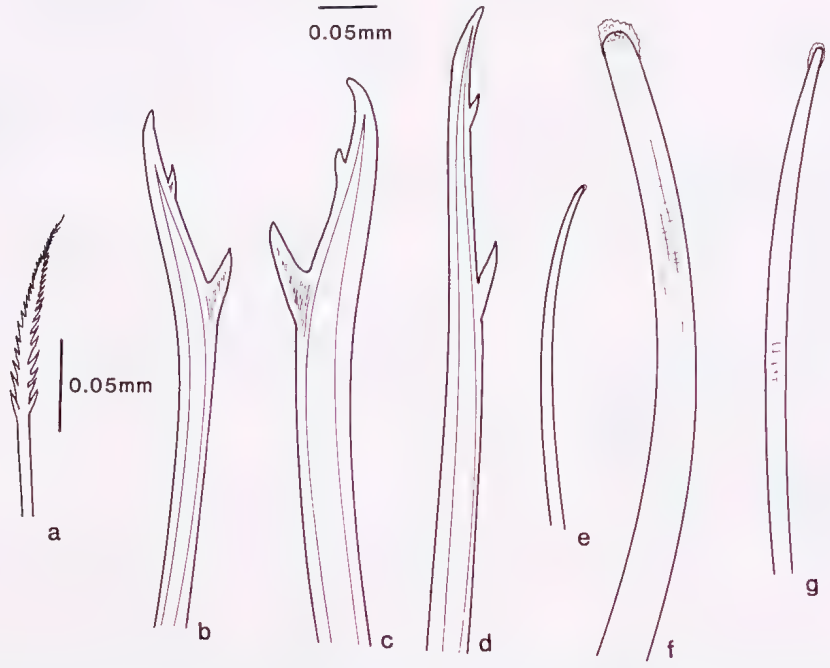

Fig.29. *Aphrogenia margaritacea* (AM W 201443): a, bipinnate neuroseta from segment 3; b, upper neuroseta from segment 3; c, neuroseta from segment 16; d, neuroseta from segment 25; e, notoseta from segment 4; f, notoseta from segment 16; g, notoseta from segment 25.

Aphrogenia nigropunctata Horst

Figs 30a,b, 60, Table 5

Aphrogenia nigropunctata Horst, 1916b: 77.–Horst, 1917: 64, pl.XIV fig.13.–Monro, 1924: 66-67.
Aphrogenia villosa var. *laevis* Horst, 1916b: 77.–Horst, 1917: 64.

Type material examined. HOLOTYPE: Indonesian Archipelago Stn 37: Paternoster Islands: Sailus Ketjil, 7°35'S 117°27'E, 27 m (ZMA V.Pol 78), 0.8 cm long, 0.55 cm wide, 29 segments. COTYPE: Indonesian Archipelago Stn 315: Paternoster Islands: Sailus Besar, 7°31'S 117°26'E, 36 m (ZMA V.Pol 2758), 0.5 cm long, 0.45 cm wide, 26 segments.

HOLOTYPE of *Aphrogenia villosa* var. *laevis* Indonesian Archipelago Stn 285: south coast of Timor, 8°39.1'S 127°4.4'E, 34 m (ZMA V.Pol 76), 0.9 cm long, 0.6 cm wide, 29 segments.

Description. Body oval, 0.5-0.9 cm long, 0.45-0.6 cm wide, 26-29 segments.

Dorsum creamy yellow in alcohol, elytra slightly opalescent. Ventral surface cream coloured, covered in rounded papillae.

Prostomium rounded with 2 large ocular lobes half length of prostomium, eye pigment absent. Median antenna with ceratophore 2-jointed three-quarters length of prostomium; style clavate-tipped, 5 times length of prostomium. Facial tubercle, small, located below ceratophore visible only ventrally, covered with cylindrical papillae. Palps extending to segment 7-8, tapering with finely papillated margins.

Elytra 14 pairs, attached by elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25 and 28. Elytra slightly opalescent with a mottled cream, yellow and brown pattern, first pair small, triangular with rounded edges with elytrophore attached centrally, following elytra large, leaf-shaped with elytrophores attached centrally, last pair small, oval with elytrophore attached laterally. All elytra covered in scattered micropapillae.

Fig.30. *Aphrogenia nigropunctata* (ZMA V.Pol 78): a, bipinnate neuroseta from segment 3; b, neuroseta from middle segment.

First or tentacular segment with elongated, uniramous parapodia, projecting anteriorly to prostomium, above palps; with aciculae and large terminal asymmetrical lobe on anterior, inner edge, covered with many cylindrical papillae; short tuft of capillary setae on dorsal surface, and tuft on medial edge fanning posteriorly, and 2 pairs of clavate-tipped cirri with large cylindrical tentaculophores, dorsal pair half length of median antenna, ventral pair one-third length of dorsal pair.

Parapodia of segment 2 and 3 biramous, neuropodia cylindrical, covered with large, rounded papillae with 2 tiers of neurosetae. Lower tier with many (20+) pale yellow, bipinnate neurosetae (Fig.30a), upper tier with 1-3 golden yellow bidentate neurosetae some with 1-2 extra teeth (Fig.30b).

Following segments with biramous parapodia. Neuropodia cylindrical, covered in large globular papillae, with 3-4 golden yellow neurosetae with slightly hooked tips and basal spur. Ventral cirri clavate-tipped not extending to distal margins of neuropodia.

Elytrigerous notopodia with tuft of 2-3 golden yellow, flattened, smooth, sabre-like notosetae with rounded mud-covered tips, fanning across dorsum; lower surface of notopodia with small tuft of fine, mud-covered, capillary notosetae.

Cirrigerous notopodia with cylindrical cirrophores on posterior edge of notopodia, styles with clavate tips longer than sabre notosetae; anterior to cirrophores a dark brown to black spot. Lateral edge of notopodia with fan of about 6 pale sabre notosetae pointing laterally; notosetae shorter than sabre notosetae of elytrigerous notopodia. Lower surface of notopodia with tuft of fine, mud-covered capillary notosetae.

Remarks. The holotype of *A. nigropunctata* was a gravid individual indicating mature size. Examination of the type material of *A. nigropunctata* and *A. villosa* var. *laevis*, revealed that this species and this variety of *A. villosa* were identical and we have therefore synonymised them.

Aphrogenia nigropunctata is characterised by only two to three sabre-like notosetae forming a fan on elytrigerous segments and can clearly be distinguished from other Indo-Pacific species (Table 5).

This species is known only from the original description.

Habitat. Trawled at depths of 27-34 m.

Distribution. Paternoster Islands, Indonesian Archipelago (Fig.60).

Aphrogenia villosa Horst

Figs 31a-c, 60, Table 5

Aphrogenia villosa Horst, 1916b: 76-77.–Horst, 1917: 63, pl.XIV figs 10-12.

Type material examined. HOLOTYPE: Indonesian Archipelago Stn 273: Aru Islands: east of Pulu Jedan, 5°23'S 134°41'E, 13 m (ZMA V.Pol 334), 1.3 cm long, 0.87 cm wide, 32 segments.

Description. Body oval, 1.3 cm long, 0.87 cm wide. 32 segments.

Dorsum with elytra tan orange in alcohol, with pale yellow notosetae fanning across them. Ventral surface tan coloured covered in spherical papillae.

Prostomium rounded with 2 ocular lobes half length of prostomium, each with pair of dark grey eyes. Median antenna with ceratophore one-third length of prostomium; style with clavate process at tip, 6 times length of prostomium. Palps extending to segment 8, tapering with papillated margins. Facial tubercle small, situated below ceratophore therefore visible only ventrally, covered in rounded papillae.

Elytra 14 pairs, attached by elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25 and 28. Elytra slightly opalescent, first pair missing, remaining elytra large, leaf-shaped with some scattered micropapillae with elytrophores attached laterally (Horst, 1917: pl.XIV fig.10).

First or tentacular segment with elongated, uniramous parapodia, projecting anteriorly to prostomium, with aciculae and large terminal asymmetrical lobe on anterior, inner edge; short tuft of capillary setae emerging radially from inner distal and ventral margins of lobe. Two pairs of clavate-tipped cirri with large cylindrical, papillated tentaculophores, dorsal pair two-thirds length median antenna, ventral pair two-thirds length of dorsal pair.

Parapodia of segment 2 and 3 biramous, neuropodia cylindrical with some (20+) bipinnate neurosetae present (Fig.31a).

Following segments with biramous parapodia. Neuropodia cylindrical, with papillated appendix on distal tip (Fig.31b), covered in large rounded papillae, with 3 golden brown neurosetae with slightly hooked tips, with basal spur (Horst, 1917: pl.XIV fig.12). Ventral cirri, with clavate tips, emerging just below distal margins of neuropodia.

Elytrigerous notopodia with fan of about 6 pale yellow, flattened, ridged, sabre-like notosetae with rounded mud-covered tips (Horst, 1917: pl.XIV fig.11) (Fig.31c), arching over dorsum, meeting mid-dorsally.

Cirrigerous notopodia with cylindrical, papillated cirrophores on posterior edge of notopodia with styles of dorsal cirri with clavate tips about half length of sabre notosetae. Dorsal surface of notopodia with fan of about 10 thin, pale sabre notosetae fanning laterally; notosetae half length of sabre notosetae of elytrigerous notopodia. Lower surface of notopodia with tuft of short, fine, mud-covered capillary notosetae.

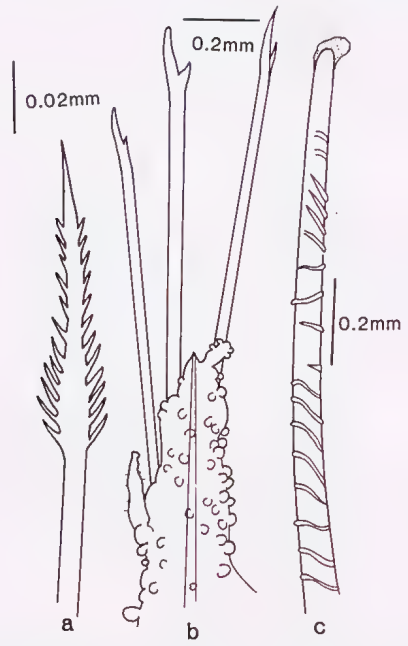

Fig.31. *Aphrogenia villosa* (ZMA V.Pol 334): a, bipinnate neuroseta from segment 3; b, neuropodia from middle segment; c, notoseta from middle segment.

Remarks. This species which is known only from the holotype is characterised by the development of ridges on the sabre-like notosetae and this character clearly distinguishes it from other Indo-Pacific species (Table 5).

Habitat. Trawled at a depth of 13 m.

Distribution. Aru Islands, Indonesian Archipelago (Fig.60).

Laetmonice Kinberg, 1856

Hermione Blainville, 1828: 457. Preoccupied, see Pettibone, 1966 for details.
Laetmonice Kinberg, 1856: 7.
Laetmatonice Kinberg, 1856: 7.
Letmonicella Roule, 1898: 191-192.
Halogenia Horst, 1916a: 63-64.–Buzhinskaja, 1982: 30.
Hermonia Neave, 1939: 625.–Hartman, 1959: 56. New name for *Hermione* Blainville, pre-occupied.–Day, 1967: 31-32.

Diagnosis. Aphroditids with dorsal feltage poorly developed, not completely covering elytra. Elytra up to 20 pairs, smooth. Prostomium with short ocular peduncles. Facial tubercle well developed, papillated. Notosetae of 3 kinds: acicular, smooth or granular, arched over dorsum; stout, long, with tips in form of barbed arrow (harpoon setae); short or long capillary setae, sometimes forming poorly developed dorsal feltage. Neurosetae dark, stout with slightly curved tips, with lateral spur, some with accessory denticles under

rostrum or with unilateral fringe of long stiff filaments. Some bipinnate neurosetae on few anterior segments.

Type species. *Laetmonice filicornis* Kinberg, 1856, by monotypy.

Remarks. We have followed the generic diagnosis given by Pettibone, (1966) and the synonymies which she suggested. The name *Hermione* Blainville, 1828 is preoccupied as pointed out by Claparède, 1868 as the name has been used by Meigen (1800) in Diptera, *fide*

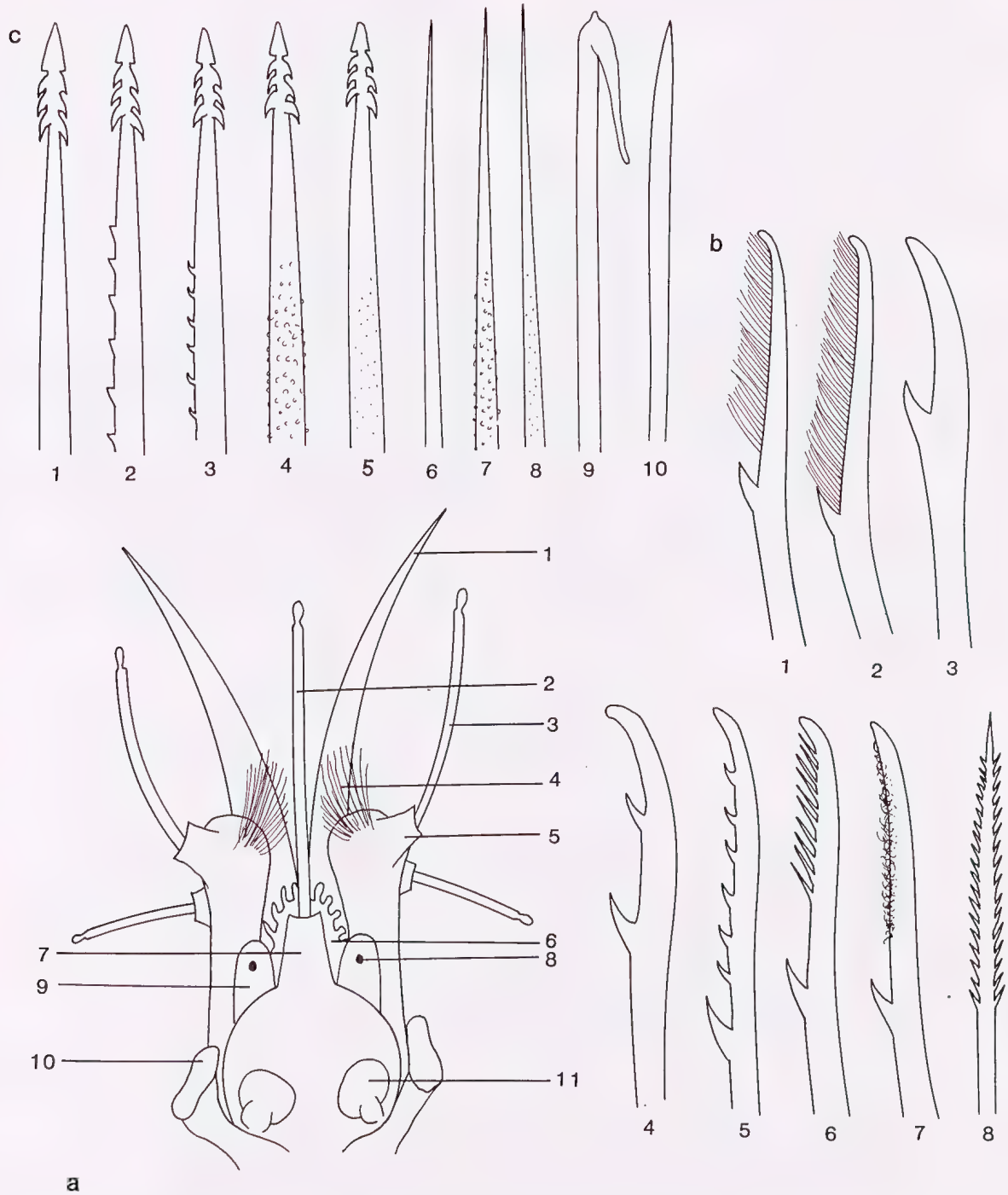

Fig.32. Generalised *Laetmonice*. a: dorsal view of prostomium and first segment – 1, palp; 2, median antenna; 3, tentacular cirrus; 4, setae; 5, tentaculophore; 6, facial tubercle; 7, ceratophore; 8, eye; 9, ommatophore; 10, elytrophore; 11, nuchal flap. b: neurosetal types – 1, basal spur with gap to distal fringe of hairs; 2, basal spur without gap to distal fringe of hairs; 3, bidentate; 4, bidentate with 1 extra tooth; 5, basal spur with many extra teeth; 6, basal spur and distal short thick hairs; 7, basal spur with plumose edge; 8, bipinnate. c: notosetal types – 1, harpoon, shaft smooth; 2, harpoon, shaft with series of thorns; 3, harpoon, shaft with acute tubercles; 4, harpoon, shaft tuberculated; 5, harpoon, shaft finely tuberculated; 6, acicular, smooth; 7, acicular, tuberculated; 8, acicular, finely tuberculated; 9, hooked; 10, developing harpoon.

Neave, 1939. Neave (1939) suggested the use of the name *Hermonia*. Buzhinskaja (1982) used the name *Halogenia*, and has therefore not accepted Pettibone's (1966) recommendations and Day (1967) continued to use the name *Hermonia* as proposed by Hartman (1959). For these reasons a synopsis is given below of the discussion given by Pettibone (1966) for the use of the name *Laetmonice*. Not only was the name *Hermione* preoccupied but there are problems with the identity of the material identified by Blainville, 1828.

Claparède (1868) suggested that the descriptions and figures of Blainville (1828) should perhaps be referred to *Pontogenia chrysocoma* (Baird, 1865) and that the preoccupied name of *Hermione* Blainville be abandoned and replaced by that of *Laetmonice* Kinberg 1856. This was not generally adopted and Hartman (1959) proposed a new name of *Hermonia* to replace the preoccupied name of *Hermione* following Neave (1939). However this did not take into account the confused identity of Blainville's type species. As no type material is available, the true identity of Blainville's species cannot be established. Pettibone (1966) quotes the work of Claparède (1868) who suggests that the species described under the name *Hermione hystrix* by Blainville was not the same as *Halithea hystrix* Savigny, in Lamarck, 1818 the type species of the genus *Hermione*. Pettibone (1966) formalised the suggestions made by Claparède (1868) that the confused name of *Hermione* Blainville be abandoned and replaced by that of *Laetmonice* Kinberg since they appeared to be generically synonymous.

The main difference between species assigned to the genus *Hermione* and *Laetmonice* according to Pettibone (1966) is the structure of the neurosetae, hooked but without a fringe of hairs in the former genus and hooked but with a fringe of hairs in the latter genus. Pettibone (1966) suggests that these are specific differences and not generic differences and we concur with her interpretation, and have therefore followed Pettibone's recommendations that species of *Hermione* Blainville, 1828 should be referred to the genus *Laetmonice* Kinberg, 1856. We believe that the following characters are important at the species level, number of segments, number of pairs of elytra, prostomial structure, presence or absence of eyes, length of ocular peduncles, palps and median antenna, type of neurosetae, and harpoon notosetae and these are discussed in detail in the Introduction of this paper.

Hartman (1956, 1965) and Hutchings (personal records) list 21 valid species of *Laetmonice* of which 16 are Indo-Pacific species. We have summarised all these characters for Indo-Pacific species where possible in Table 6. As with the genus *Aphrodita* many of the early descriptions are brief and not all these characters are discussed although in some cases they can be inferred from the figures given. In Figure 32 we provide a labelled stylised *Laetmonice* and setal types to indicate the various structures described in the text. Some harpoon notosetae from anterior segments are smooth and not exhibiting the recurved fangs, such as in *L. producta* and *L. malayana*.

Key to the Indo-Pacific Species of *Laetmonice*

1. Hooked type notosetae present (Figs 33f,37c) 2

—— Hooked type notosetae absent 3

2. Neurosetae with basal spur and distal short thick hairs (Fig.33c) ..... *Laetmonice arenifera*

—— Neurosetae with basal spur and 2-3 extra teeth (Fig.37b) ..... *Laetmonice conchifera*

3. Neurosetae with basal spur and fringe of distal hairs (Fig.46c,d); or fringe reduced to short pinnae or plumose edge (Fig.36d) 4

—— Neurosetae with basal spur and with one or more distal teeth (Figs 44b, 47b) 10

4. Neurosetae with basal spur and distal fringe of long hairs (Fig.46c,d) 5

—— Neurosetae with basal spur and distal plumose edge (Fig.36c,d); small appendix on distal margin of neuropodia (Fig.35b) ..... *Laetmonice brachyceras*

5. 18 or more pairs of elytra ..... *Laetmonice producta*

—— Up to 15 pairs of elytra 6

6. Prostomium with pair of purse-like nuchal flaps on posterior edge of prostomium (Fig.49a) ..... *Laetmonice wonda* n.sp.

—— Prostomium without purse-like nuchal flaps 7

7. Neurosetae without gap between basal spur and distal fringe (Fig.48c) ..... *Laetmonice viridescens*

—— Neurosetae with gap between basal spur and distal fringe (Fig.40b,c) 8

8. Harpoon notosetae with shafts beset with a series of thorns (Fig.40g,i) ..... *Laetmonice malayana*

—— Harpoon notosetae with shafts smooth or beset with acute tubercles 9

9. Harpoon notosetae with shafts smooth (Fig.51g) ..... *Laetmonice yarramba* n.sp.

—— Harpoon notosetae with shafts beset with acute tubercles (Fig.34c) ..... *Laetmonice batheia*

10. Neurosetae with basal spur and 1-3 distal teeth (Fig.44b); palps papillated 11

—— Neurosetae with basal spur and 3-5 distal teeth (Fig.47b); palps smooth ..... *Laetmonice rugosa*

11. Harpoon notosetae and notosetal spines with shafts finely tuberculated (Fig.44c) ..... *Laetmonice parva*

—— Harpoon notosetae and notosetal spines with shafts smooth 12

12. Elytra completely covered by notosetae; harpoon notosetae directed dorsally ..... *Laetmonice moluccana*

—— Elytra not completely covered by notosetae; harpoon notosetae directed posteriorly ..... *Laetmonice dolichoceras*

Laetmonice arenifera (Horst)

Figs 33a-g, 60, Table 6

Halogenia arenifera Horst, 1916a: 63, fig.1.–Horst, 1917: 60, pl.XII figs 17-19.
Laetmonice arenifera Pettibone, 1966: 97.

Type material examined. HOLOTYPE: Indonesian Archipelago Stn 49A: East Sapeh Strait, 8°23.5'S 119°4.6'E, 69 m (ZMA V.Pol 343), 1.3 cm long, 1 cm wide, 31 segments.

Description. Body elongate, oval, 1.3 cm long, 1 cm wide. 31 segments.

Dorsum tan coloured in alcohol, with long golden brown notosetae on lateral edge, without felt covering elytra. Ventral surface tan coloured, covered thickly with spherical papillae.

Prostomium rounded with 2 ocular peduncles, one-third length of prostomium, Horst (1917) states that a large black eye spot present, not visible now, probably faded in alcohol storage. Median antenna with short 2-jointed ceratophore, style missing. Palps long, tapering, finely papillated, extending to segment 10. Facial tubercle small situated below ceratophore therefore visible only ventrally, covered in cylindrical papillae.

Elytra 15 pairs, attached to elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra thin, semi-transparent, fragile, first pair missing, following elytra larger, leaf-shaped, attached to elytrophores laterally, posterior pairs small, oval, attached to elytrophore anterolaterally.

First or tentacular segment with elongated uniramous parapodia, projecting anteriorly and laterally to prostomium, enlarged distally, forming rounded lobe, with tuft of short, mud-covered setae, emerging from medial and dorsal margins. Two pairs of tentacular cirri with cylindrical tentaculophores and styles long,

slender, clavate-tipped, dorsal pair 3 times length of prostomium, ventral pair three-quarters length of dorsal pair.

Following segments with biramous papapodia. Second, third and fourth neuropodia with 2 tiers of neurosetae. Lower tier consisting of numerous (20+) golden yellow, bipinnate neurosetae (Fig.33a); upper tier with 1-2 golden yellow neurosetae with basal spur short, thick hairs (Fig.33b).

Remaining neuropodia cylindrical, papillated. Neuropodia with 3 golden yellow neurosetae with basal spur and fringe of short, thick hairs (Horst, 1917: pl.XII fig.19) (Fig.33c). Ventral cirri long, tapering, arising in middle of neuropodia, not extending to distal tip of neuropodia.

Elytrigerous notopodia with tuft of short, pale yellow, unidentate notosetae, one-fifth length of harpoon notosetae also fine capillary notosetae entrapping many large sand grains. Lateral to this tuft bundle of about 10 harpoon notosetae, directed posterolaterally, with shafts smooth, tapering abruptly below tip with 2-3 recurved fangs on lateral margins, some tips covered with gelatinous sheaths (Horst, 1917: pl.XII fig.18) (Fig.33d,e). Harpoon notosetae intermingled with 20 or more thin, notosetae with pale shafts and brown hooked tips (Horst, 1917: pl.XII fig.17) (Fig.33f,g).

Cirrigerous notopodia with cylindrical cirrophore, dorsal cirri long, clavate tipped, one-third length of harpoon notosetae. Dorsal surface of notopodia with fan of pale yellow, unidentate notosetae and tuft of capillary notosetae entrapping large sand grains.

Remarks. Pettibone (1966) synonymised *Halogenia* Horst (1916a) with *Laetmonice* Kinberg 1856, and Hartman (1959) had designated *Halogenia arenifera* Horst, 1916a as the type species of the genus. Horst described *H. arenifera* as belonging to a new genus because although it closely resembled *Laetmonice*, it differed in the shape of the notosetae. These notosetae we regard as just another type of notosetae, and this single character is insufficient to warrant the retention of the genus *Halogenia* and we agree with Pettibone's synonymy of this genus with *Laetmonice*. She states that Horst's publication date was 1915, whereas the publication is clearly dated 1916.

We have expanded Horst's original description to give details on the numbers of setae present. Horst (1917) states that there is a folded ridge at right and left hand side of the prostomium, and these are the elytrophores of segment 2. The species is known only from the holotype. This species can be separated from other described species of *Laetmonice* by the presence of hooked type notosetae and neurosetae with a basal spur and distal fringe of thick hairs which distinguishes it from other described species of *Laetmonice*, see Table 6.

Habitat. Trawled at 69 m.

Distribution. Indonesian Archipelago (Fig.60).

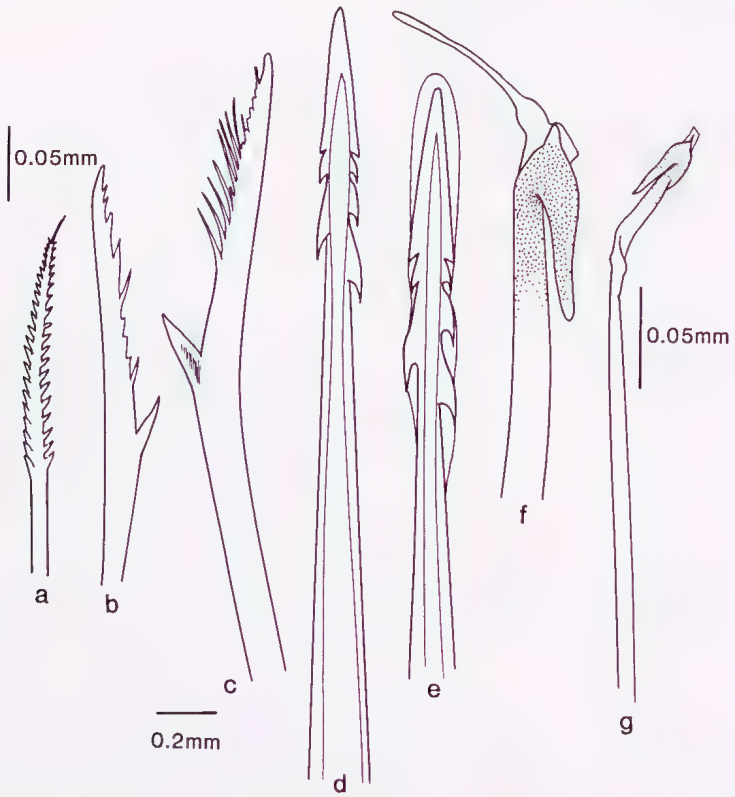

Fig.33. *Laetmonice arenifera* (ZMA V.Pol 343): a, bipinnate neuroseta from segment 3; b, upper neuroseta from segment 3; c, neuroseta from middle segment; d, harpoon notoseta from middle segment; e, tip of harpoon showing sheath; f, tip of hooked notoseta; g, hooked notoseta.

Laetmonice batheia Horst

Figs 34a-c, 60, Table 6

Laetmonice batheia Horst, 1916b: 75-76.–Horst, 1917: 58, pl.XIII figs 14,15.

Type material examined. LECTOTYPE: Indonesian Archipelago Stn 221: east-south-east of Binongka Island, 6°24'S 124°39'E, 2798 m (ZMA V.Pol 482), 2.6 cm long, 0.9 cm wide, 33 segments.

Description. Body elongate, oval, 1.9 cm long not including notosetae, 2.6 cm long including notosetae, 0.9 cm wide. 33 segments.

Dorsum cream coloured in alcohol. Horst (1917) states a mud-covered dorsal felt occurs, this was not observed on the lectotype probably due to the poor condition of the specimen. Ventral surface creamy yellow, covered with small spherical papillae.

Prostomium rounded with 2 ocular peduncles, without eye pigment, half length of prostomium. Median antenna with thick ceratophore, half length prostomium, style missing. Palps long, tapering, finely papillated, extending to segment 14. Facial tubercle small, situated below median antenna, visible only ventrally, covered in small rounded papillae.

Fig.34. *Laetmonice batheia* (ZMA V.Pol 482): a, bipinnate neuroseta from segment 2; b, upper neuroseta from segment 2; c, harpoon notoseta from middle segment.

Elytra 14 pairs (Horst, 1917 states 12 pairs present), attached to elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25 and 28. Elytra smooth, semi-transparent, first pair missing, following elytra rounded, attached to elytrophores laterally, posterior elytra small, oval, attached to elytrophore laterally.

First or tentacular segment with short uniramous parapodia equal to length of prostomium, projecting anteriorly and laterally to prostomium, enlarged distally, forming rounded lobe, with tuft of short capillary setae, emerging radially from medial to posterior margins. Two pairs of cylindrical tentaculophores, all tentacular cirri missing.

Following segments with biramous parapodia. Second, third and fourth neuropodia with 3 tiers of neurosetae. Lower tier consisting of numerous (20+) golden yellow, bipinnate neurosetae (Fig.34a); middle tier with 3-4 neurosetae with basal spur and 8-16 extra teeth; upper tier with 2 golden yellow neurosetae with basal spur and 8-16 extra teeth (Fig.34b).

Remaining neuropodia cylindrical, smooth, with 3 golden yellow neurosetae. Neurosetae with basal spur and gap to distal fringe (Horst, 1917: pl.XIII fig.15). Ventral cirri long, thin, arising from medial edge of ventral surface of neuropodia, extending below distal margins of neuropodia.

Elytrigerous notopodia with short tuft of 10 or more, fine, pale yellow, mud-covered notosetae, one-quarter length of harpoon notosetae, pointing posteriorly. Lateral to this tuft occurs tuft of 5, golden brown harpoon notosetae with darker tips. Harpoon notosetae extending past posterior edge of body, with shafts scattered with acute tubercles, tips with 3 recurved fangs on lateral margins (Fig.34c).

Cirrigerous notopodia with cylindrical cirrophores, with tuft of many short, pale yellow, mud-covered, unidentate notosetae pointing laterally.

Remarks. This species is only known from two individuals examined by Horst (1916b, 1917) of which only one was available for examination. We have considerably expanded the original description although the original felt appears to be lost, and the specimen examined is not in good condition.

This species is characterised by harpoon shaped notosetae with shafts ornamented by tubercles, which distinguishes it from other species of *Laetmonice*, see Table 6.

Habitat. Trawled at 2798 m.

Distribution. Binongka Island, Indonesian Archipelago (Fig.60).

Laetmonice brachyceras (Haswell)

Figs 35a-f, 36a-j, 59F, 60, Table 6

Hermione brachyceras Haswell, 1883: 272, pl.VII figs 1-3.

Hermonia brachyceras Hartman, 1959: 56.

Laetmonice breve-pinnata Horst, 1916b: 75.–Horst, 1917: 57-58, pl.XIII fig.13.–Monro, 1924: 65-66, figs 1,2.

Type material examined. HOLOTYPE: Australia: Queensland:

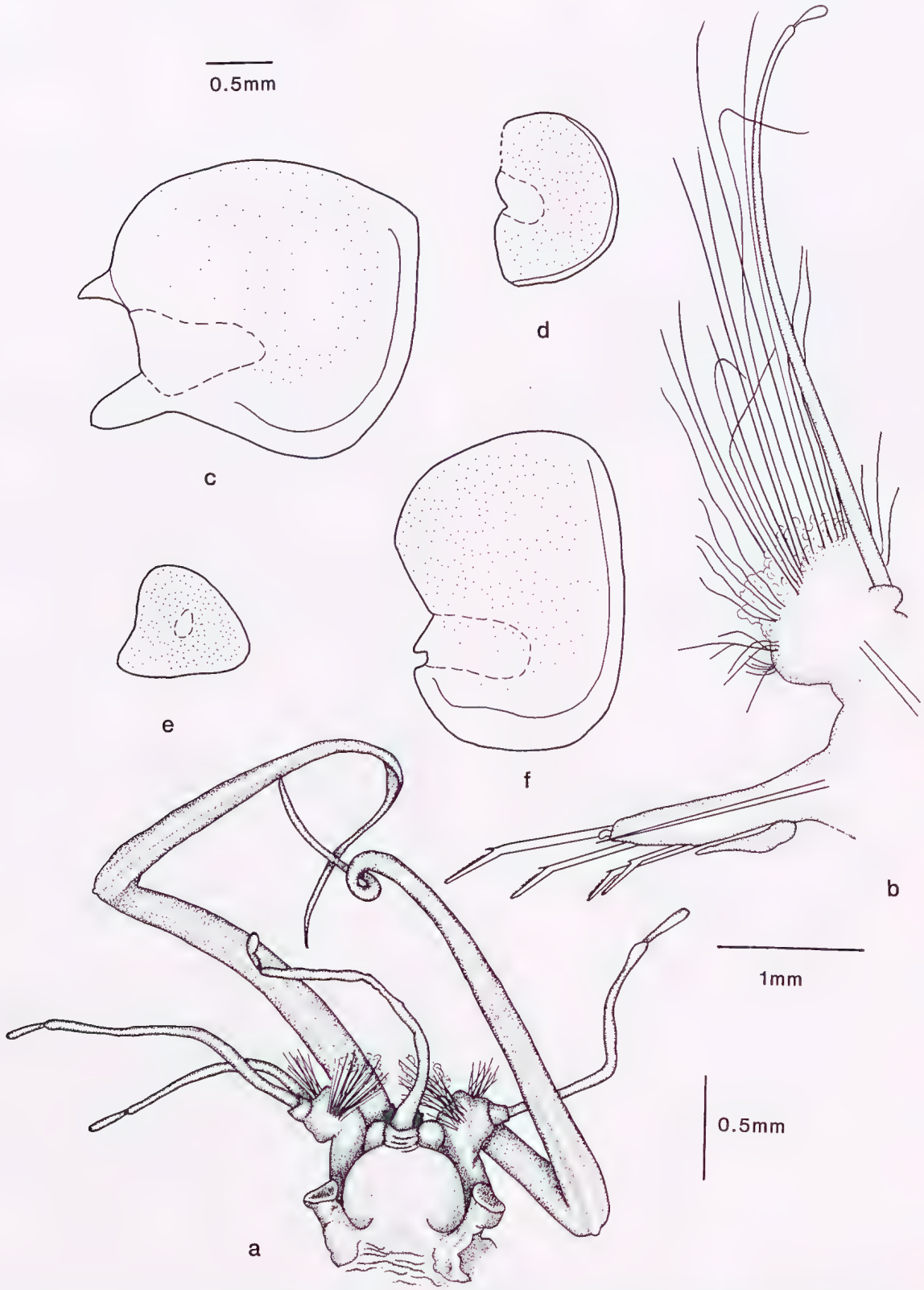

Fig.35. *Laetmonice brachyceras* (AM W20189): a, dorsal view of prostomium and first segment; b, posterior view of parapodium 16; c, (NTM W271) eighth elytron; d, third elytron; e, first elytron; f, 14th elytron.

Port Molle, 20°20'S 148°51'E, Sept. 1908 (AM G11241), 2.1 cm long.

Additional material examined. NORTHERN TERRITORY: Oxley Island, 11°00'S 138°48.5'E, 21 Oct. 1982, 15 m, 2(NTM W0272), 1.3-1.45 cm long; Oxley Island, 11°00'S 138°48.5'E, 21 Oct. 1982, 15 m, 3(NTM W271), 1.2-2.6 cm long. WESTERN AUSTRALIA: Port Hedland, 20°18'S 118°35'E, 24 Oct. 1983, 36-37 m (AM W20188), 0.8 cm long. QUEENSLAND: Bowen, 19°53'S 148°05'E, 11 June 1983, 15.5-17 m (AM W20187), 3 cm long; Bowen, 19°53'S 148°05'E, 19 June 1982, 5-6 m (AM W20189), 1.9 cm long.

HOLOTYPE, *Laetmonice breve-pinnata*, Indonesian Archipelago Stn 311: Sapeh Bay: East coast of Sumbawa, 8°30'S 117°25'E, 36 m (ZMA V.Pol 483), 2.7 cm long, 1.2 cm wide, 36 segments.

Description. Body cigar shaped, 0.8-3 cm long, 0.6-1.2 cm wide, 34-36 segments.

Dorsum cream coloured in alcohol, without felt covering elytra. Ventral surface creamy yellow, transparent, covered with minute spherical papillae.

Prostomium rounded with 2 small ocular peduncles, without eye pigment, one-quarter length of prostomium. Median antenna with short ceratophore, style long, 2-4 times length of prostomium, slender, tapering with clavate tip (missing on holotype, but scar visible). Palps long, tapering, smooth, extending to segment 9-11. Facial tubercle small, situated below median antenna, visible only ventrally, covered in small cylindrical papillae (Fig.35a).

Elytra 15 pairs, attached on elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra thin, transparent, faintly iridescent, first pair small, triangular with rounded edges, with elytrophore attached centrally, following elytra large, oval to leaf-shaped, with elytrophores attached laterally, posterior elytra small, rectangular with rounded edges with elytrophore attached anterolaterally (Fig.35c-f).

First or tentacular segment with elongated uniramous parapodia, projecting anteriorly and laterally to prostomium, enlarged distally, forming rounded lobe, with tuft of short, yellow, mud-covered setae, emerging radially from distal margins. Two pairs of long slender, clavate-tipped tentacular cirri, dorsal pair one-quarter length of palps, ventral pair shorter than dorsal pair (Fig.35a).

Following segments with biramous papapodia (Fig.35b). Second, third and fourth neuropodia with 2 tiers of

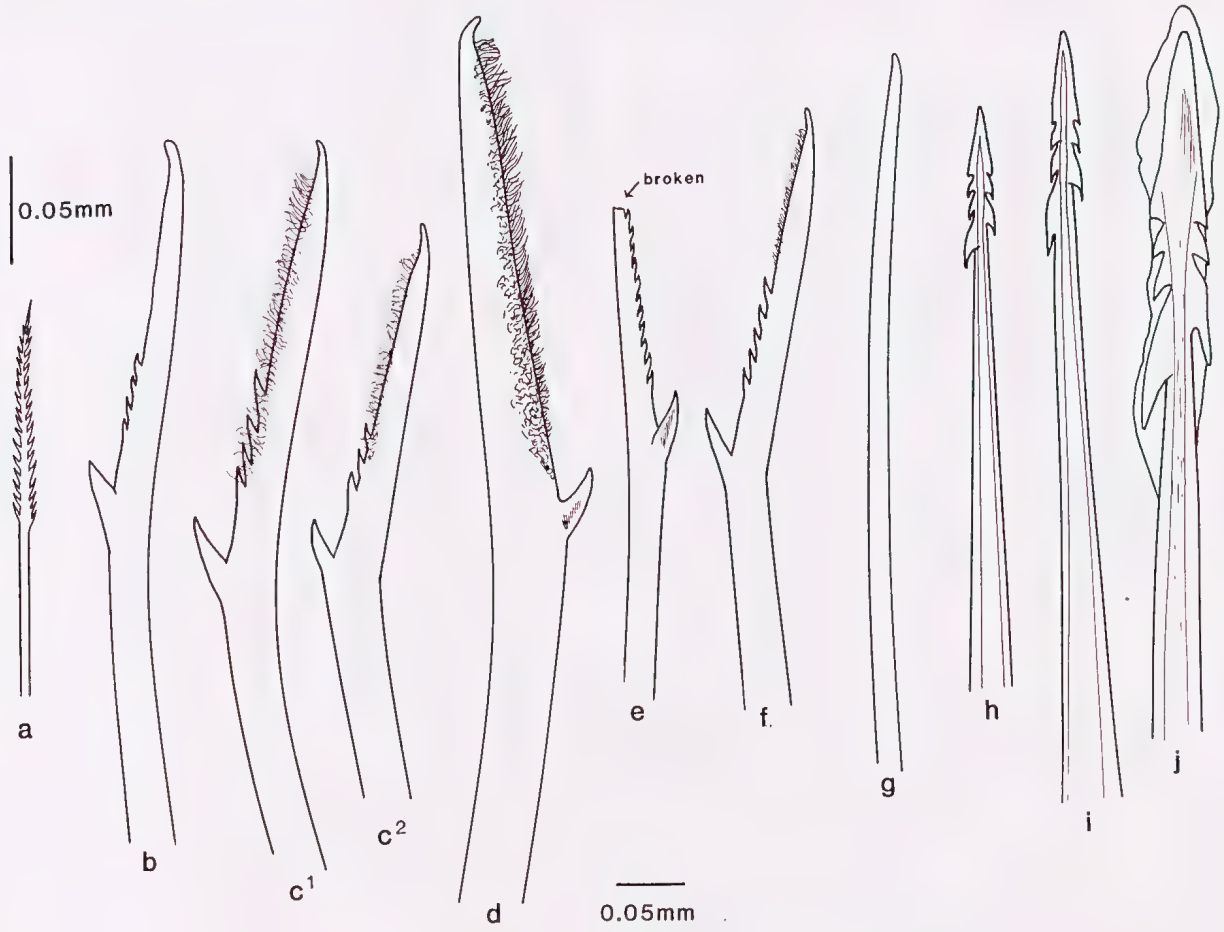

Fig.36. *Laetmonice brachyceras* (NTM W271): a, bipinnate neuroseta from segment 3; b, neuroseta from segment 4; $c^{1,2}$, neuroseta from middle segment; d, neuroseta from segment 16; e, neuroseta from segment 32; f, posterior neuroseta; g, acicular notoseta from segment 4; h, harpoon notoseta from segment 5; i, harpoon notoseta from segment 17; j, tip of harpoon showing sheath.

neurosetae. Lower tier consisting of numerous (30+) golden yellow, bipinnate neurosetae (Fig.36a); upper tier with 2-3 golden yellow neurosetae with long shaft, smooth or finely plumose with short pinnae, one-third below unidentate tip, with basal spurs and distal teeth. Ventral cirri swollen basally, with tapering tips, extending just past distal margins of neuropodia.

Remaining neuropodia cylindrical, smooth, with small curved appendix emerging from distal tip (Fig.35b). Neuropodia with 2-4 golden yellow neurosetae of varying types, anterior ones with basal spur and 4-7 distal teeth (Fig.36b), middle neurosetae with basal spur, pilose edge and 1-4 extra teeth (Fig.36c[1,2],d), posterior neurosetae with basal spur and 5-11 distal teeth, sometimes with pilose edge (Fig.36e,f). Ventral cirri swollen basally with tapering tips, extending to just below distal margin of neuropodia.

Elytrigerous notopodia with dorsal fan of 6-8 fine, pale yellow, smooth notosetae (Fig.36g), and below tuft of 10 or more, dark brown, harpoon notosetae pointing posterolaterally, with shafts smooth, tapering abruptly below tip with 2-4 recurved fangs on lateral margins forming harpoon tips, many tips covered in transparent sheaths (Fig.36h-j). Lower surface of notopodia with tuft of short, fine, yellow notosetae.

Cirrigerous notopodia dorsal cirri with clavate tips as long as notosetae, with tuft of yellow, unidentate, mud-covered notosetae, harpoon notosetae lacking. Ventral surface of notopodia with short tuft of fine, yellow, unidentate notosetae.

Remarks. This species is the same as *Laetmonice breve-pinnata* Horst (1916b, 1917), which has also been reported by Monro (1924), based on the presence of similar neurosetae, the thick ventral cirri, and the small appendix on the tip of the neuropodia. This combination of characters has not been reported in any other described species of *Laetmonice* although *L. dolichoceras* (Haswell) has a small appendix on the tip of the neuropodia. For these reasons we have synonymised the two species. We have not examined Monro's (1924) material and for this reason we have marked the record in the distribution of the species with an asterisk.

The holotype of *H. brachyceras* is not in a good condition, with many setae broken, therefore the description is a composite one, based upon the holotype and other material examined.

Habitat. One specimen was found in sand, trawled at depths of 5-37 m.

Distribution. Australia (Port Hedland, WA, 20°18'S 118°35'E to Bowen, Qld, 19°53'S 148°05'E, Fig.59F). Soembawa, Indonesian Archipelago (Horst, 1916b) (Fig.60). Hong Kong* (Monro, 1924).

Laetmonice conchifera (Horst)

Figs 37a-c, 60, Table 6

Halogenia conchifera Horst, 1916a: 64, fig.2.–Horst, 1917: 60-61, pl.XII figs 20,21.

Type material examined. HOLOTYPE: Indonesian Archipelago Stn 334: west of Great Kei Island, 5°36'S 132°55.2'E, 90 m (ZMA V.Pol 344), 0.95 cm long, 0.7 cm wide, 28 segments.

Description. Body ovate, 0.95 cm long, 0.7 cm wide, 28 segments.

Dorsum creamy yellow in alcohol, fine, sand encrusted felt covering elytra. Ventral surface cream coloured covered with small rounded papillae.

Prostomium rounded with 1 pair of small rounded ocular peduncles, one-third length of prostomium, eye pigment absent. Ceratophore of median antenna half length of prostomium, style slender, clavate-tipped, 5 times length of prostomium. Facial tubercle papillated, located below ceratophore visible only ventrally. Palps smooth, tapering, extending to segment 6.

Elytra 15 pairs, attached on elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra thin, transparent, first pair small, rounded, elytrophore attached centrally, following elytra large, leaf-shaped with elytrophore attached laterally, posterior pairs small, elongated with elytrophore attached anteriolaterally.

First or tentacular segment with uniramous parapodia,

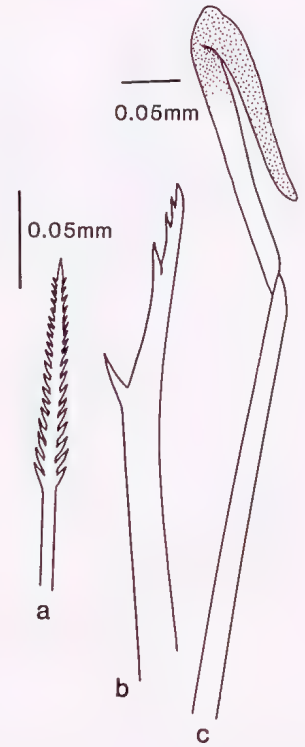

Fig.37. *Laetmonice conchifera* (ZMA V.Pol 344):a, bipinnate neuroseta from segment 3; b, neuroseta from middle segment; c, hooked notoseta from middle segment.

projecting anteriorly and laterally to prostomium, enlarged distally, forming rounded lobe, with tuft of short, fine, mud-covered setae, emerging from medial to posterior margins. Two pairs cylindrical tentaculophores with style of dorsal tentacular cirri long, slender, clavate-tipped, one and one-quarter times length of prostomium, ventral tentacular cirri missing.

Following segments with biramous parapodia, second, third neuropodia with 2 tiers of neurosetae. Lower tier consisting of numerous (20+) golden yellow bipinnate neurosetae (Fig.37a); upper tier with 1-2 golden yellow neurosetae with basal spur and 4 extra teeth. Ventral cirri on segment 2 slender, tapering, arising at base of neuropodia, extending past distal margins of neuropodia. Ventral cirri on segment 3 arising in middle of neuropodia, extending past distal margins of neuropodia.

Remaining neuropodia cylindrical, elongate, papillated with 2-3 pale yellow neurosetae, with basal spur and 2-3 extra teeth (Horst, 1917: pl.XII fig.21) (Fig.37b). Ventral cirri slender, swollen basally, tapering to blunt tip, arising from middle of neuropodia, not extending to distal tip of neurosetae.

Elytrigerous notopodia with short tuft of fine capillary notosetae, entrapping mud and sand grains. Lateral to this tuft, a tuft of about 20 hooked notosetae on anterior lateral edge of notopodia, pointing laterally, stems pale yellow, smooth, hooked tips reddish brown (Horst, 1917: pl.XII fig.20) (Fig.37c). Harpoon notosetae absent.

Cirrigerous notopodia with cylindrical cirrophores, dorsal cirri clavate-tipped, 2 times length of hooked notosetae. Ventral side of notopodia with fan of pale yellow, mud-covered notosetae, directed laterally. Dorsal surface of notopodia with tuft of mud-covered notosetae.

Remarks. This species was originally described as *Halogenia conchifera*, and Pettibone (1966) synonymised the type species of *Halogenia*, *H. arenifera* Horst (1916a) with *Laetmonice*. *H. conchifera* is also a species of *Laetmonice* and we have transferred it to this genus as the type of notosetae present resemble those found in *L. arenifera*. For additional comments on the synonymising of the genus *Halogenia* with *Laetmonice*, see the Remarks section of *L. arenifera*. The species is known only from the holotype and we have considerably expanded the description of the species.

Laetmonice conchifera is characterised by the presence of hooked-shaped notosetae, absence of harpoon type notosetae and neurosetae with a basal spur and 2-3 distal teeth, and these characters distinguish it from other described species of *Laetmonice*, see Table 6.

Habitat. Trawled at a depth of 90 m.

Distribution. Indonesian Archipelago (Fig.60).

Laetmonice dolichoceras (Haswell)

Figs 38a-f, 39a-k, 59E, Table 6

Hermione (Aphrogenia) dolichoceras Haswell, 1883: 273-274, pl.VII figs 4-7.

Aphrogenia dolichoceras Hartman, 1959: 54.–Day & Hutchings, 1979: 85.

Type material examined. HOLOTYPE: Australia: Queensland: Port Molle, 20°20'S 148°51'E, Sept. 1908, 27.4 m (AM G11285), 2.1 cm long.

Additional material examined. QUEENSLAND: Lizard Island, 14°40'S 145°28'E, 1978 (AM W20234), 1.2 cm long.

Description. Body elongate, oval, 2.5 cm long, 0.8 cm wide. 35 segments.

Dorsum creamy grey in alcohol, no felt covering elytra. Ventral surface pale tan, covered with large globular papillae.

Prostomium rounded with 1 pair of rounded ocular peduncles, half length of prostomium, 2 pairs of eyes, small dorsal pair faint grey, larger ventral pair dark grey. Ceratophore of median antenna equal to length of prostomium, style slender with clavate tip, longer than palps (missing on holotype). Facial tubercle located below ceratophore visible only ventrally, covered with cylindrical papillae. Palps, extending to segment 8, tapering finely papillated (Fig.38a).

Elytra 15 pairs, attached on elytrophores of segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra cream coloured, semi-transparent, slightly iridescent in alcohol, fragile, first pair rounded, attached medially on elytrophore, following elytra larger, leaf-shaped attached laterally on elytrophores, posterior elytra elongated with elytrophores attached anterolaterally. All elytra covered with many micropapillae (Fig.38c-f).

First or tentacular segment with flattened, uniramous parapodia, covered with cylindrical papillae on ventral surface, tuft of yellow setae on anterior end of dorsal surface, and short tuft of setae on ventral surface. Two pairs of tentacular cirri occurring dorsally and ventrally with long, cylindrical tentaculophores, styles long tapering with clavate tips (only left ventral present on outer edge of parapodia).

Following segments with biramous parapodia (Fig.38b). Second and third neuropodia with 2 tiers of neurosetae; lower tier consisting of numerous (20+) bipinnate neurosetae (Fig.39a); upper tier with 2 neurosetae. Ventral cirri slender, tapering, arising from base of neuropodia, extending past distal margins of neuropodia. Notopodia small, rounded with short tuft of pale yellow notosetae.

Remaining neuropodia elongate, covered with large globular papillae with 3 golden yellow neurosetae with basal spur, slightly curved tip with 1-3 distal teeth (Fig.39b,c). Neurosetae of anterior and posterior segments more elongated (Fig.39d). Ventral cirri arising just below

most ventral neurosetae, not extending past distal tip of neuropodia.

Elytrigerous notopodia with fan of 6 pale yellow notosetal spines (Fig.39f,h,j), fanning across elytra, not covering elytra completely. Lateral to this fan tuft of 17 or more, golden yellow, harpoon notosetae, length of body width, directed posteriorly along lateral edge of body. Harpoon tips with 2-4 recurved fangs on lateral margins (Fig.39e,g,i), many tips covered in transparent sheaths (Fig.39k), shafts smooth.

Cirrigerous notopodia with cylindrical cirrophores of dorsal cirri located on posterior side of notopodia, styles clavate-tipped, length of harpoon notosetae (all cirri missing on holotype). Ventral side of notopodia with tuft of pale yellow notosetae, directed posterolaterally.

Variation. Additional material examined 1.2 cm long, 0.6 cm wide, and 32-35 segments.

Remarks. The elytra on the holotype are extremely fragile, presumably a result of long term storage in alcohol.

In their literature review, Day & Hutchings (1979) indicate that *Hermione dolichoceras* belongs in the genus *Aphrogenia* and that this was substantiated by Kudenov (personal communication). However, it appears that Kudenov never published his justification for this transfer of the species to the genus *Aphrogenia* and our examination of the type indicates that it clearly belongs in the genus *Laetmonice* rather than *Aphrogenia* because of the presence of harpoon notosetae. *Aphrogenia* is characterised by sabre-like smooth notosetae. *Laetmonice dolichoceras* is characterised by 15 pairs of elytra, not covered by felt, notosetae which are bidentate although some have accessory teeth, and harpoon notosetae with recurved fangs covered in sheaths (Table 6).

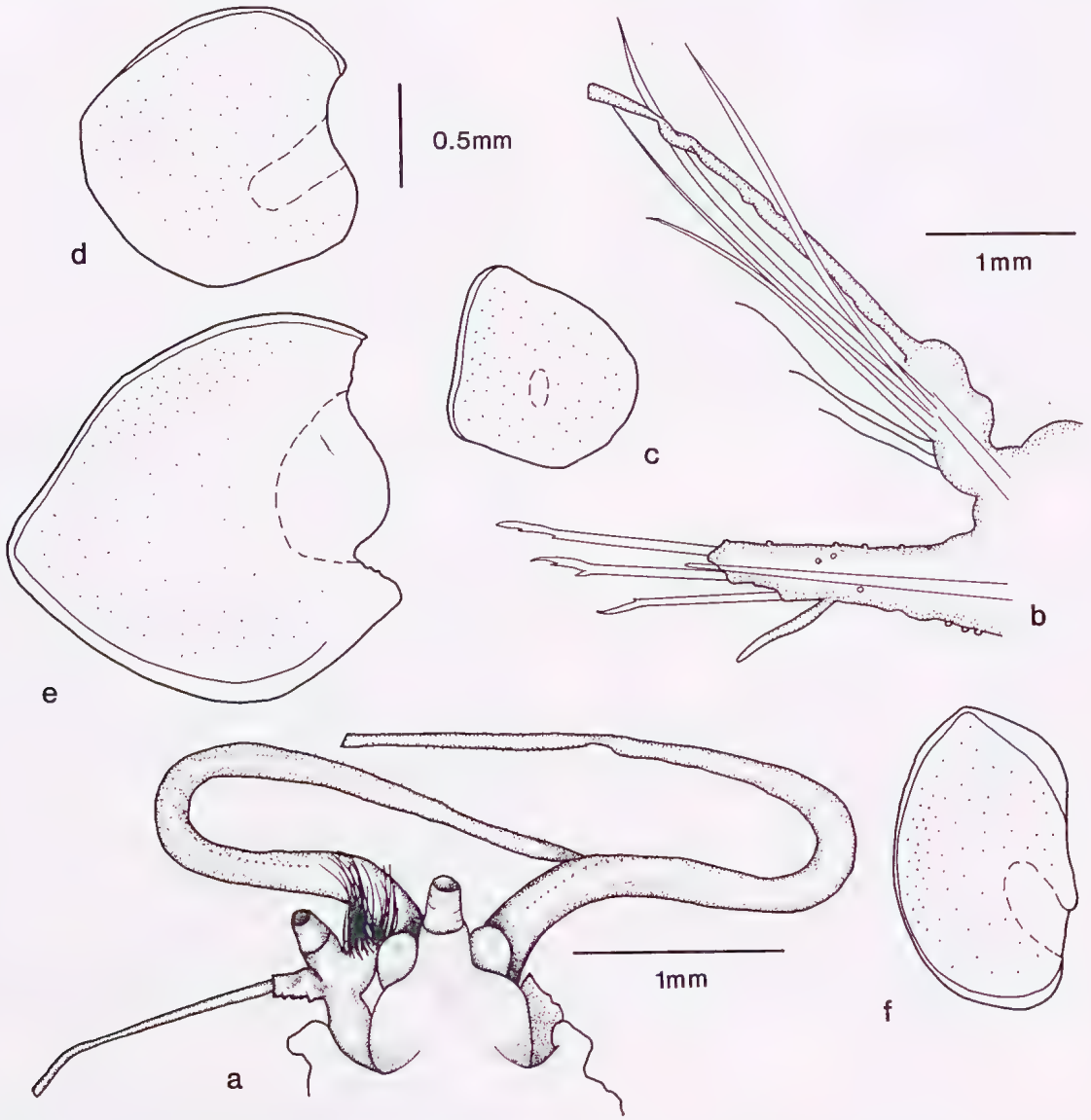

Fig.38. *Laetmonice dolichoceras*. Holotype (AM G11285): a, dorsal view of prostomium and first segment; b, posterior view of parapodium 16; c, (AM W20234) first elytron; d, third elytron; e, eighth elytron; f, 14th elytron.

Habitat. Trawled at a depth of 27.4 m.

Distribution. Australia (Port Molle, Qld, 20°20'S 148°51'E to Lizard Island, Qld, 14°40'S 145°28'E, Fig.59E).

Laetmonice malayana Horst

Figs 40a-n, 60, Tables 6, 7

Laetmonice malayana Horst, 1916b: 73-74.–Horst, 1917: 56, pl.XIII figs 4-6.

Type material examined. LECTOTYPE: Indonesian Archipelago Stn 161: north off Misool, 1°10.5'S 130°9'E, 798 m (ZMA V.Pol 486.4), 5 cm long, 2.2 cm wide, 34 segments. PARALECTOTYPES: Indonesian Archipelago Stn 52: south off Flores, 9°3.4'S 119°56.7'E, 959 m, 4(ZMA V.Pol 486.3), 3.5-3.8 cm long, 2.1-2.5 cm wide, 33 segments; Stn 178: north off Ceram, 2°40'S 128°37.5'E, 835 m, 14(ZMA V.Pol 486.1), 1.5-2.7 cm long, 0.6-2 cm wide, 31-34 segments; Stn 161: north off Misool, 1°10.5'S 130°09'E, 798 m (ZMA V.Pol 486.2), 4.3-4.5 cm long, 2-2.6 cm wide, 34 segments.

Description. Body elongate oval, 1.5-4.5 cm long, 0.8-2.5 cm wide, 30-34 segments.

Dorsum cream coloured in alcohol, no felt covering elytra. Ventral surface creamy yellow, covered with minute papillae.

Prostomium rounded with rounded ocular peduncles two-thirds length of prostomium, eye pigment absent. Median antenna with ceratophore half length of prostomium, style, long, slender, blunt tipped 3 times length of prostomium. Palps extending to segment 9-10, finely papillated. Facial tubercle located below ceratophore visible ventrally, covered in small cylindrical papillae.

Elytra 15 pairs, attached on elytrophores of segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28, then 31. Elytra thin, semi-transparent slightly overlapping, meeting mid-dorsum or leaving mid-dorsum uncovered, first pair small, rounded with elytrophore attached centrally, following elytra large, ovoid, with elytrophores

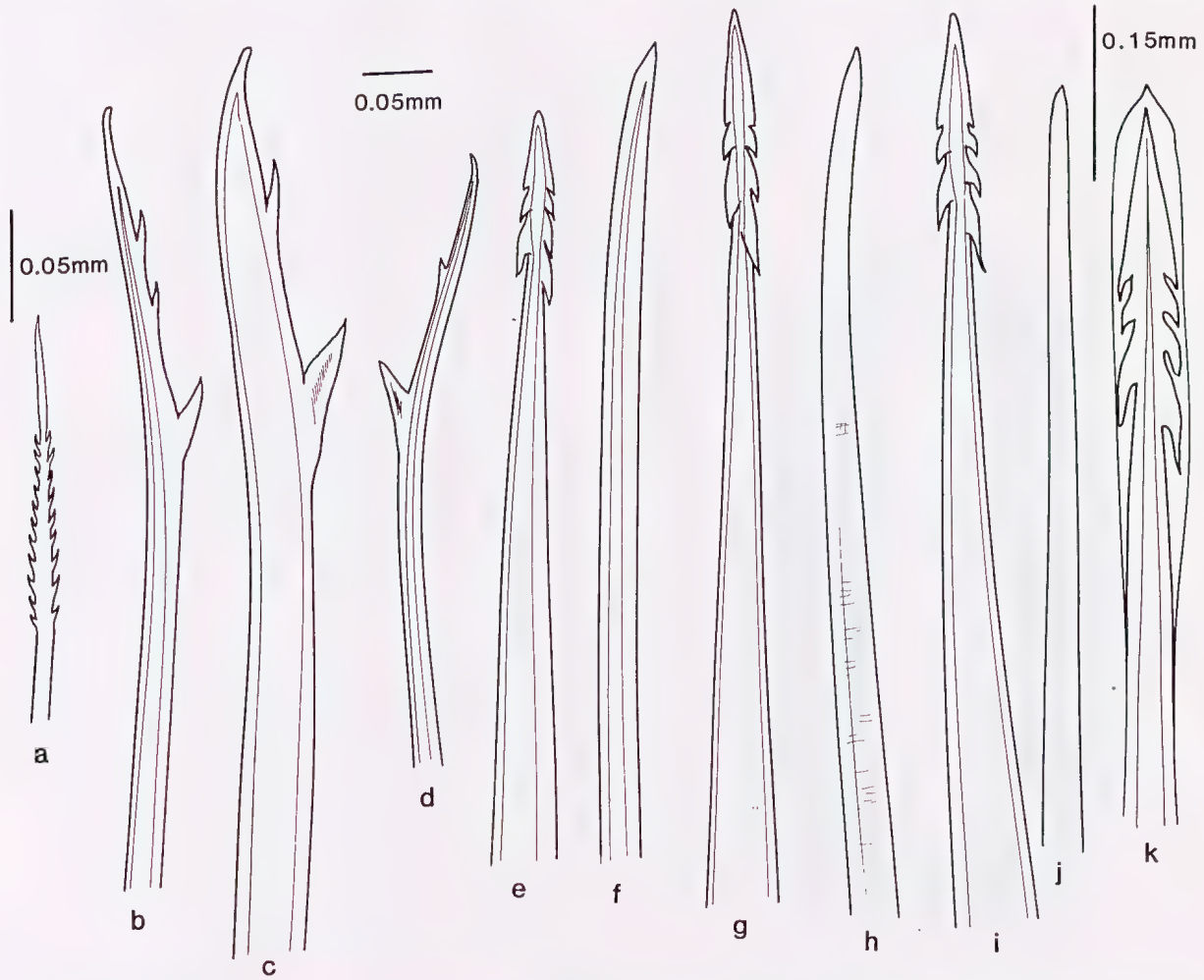

Fig.39. *Laetmonice dolichoceras* (AM W20234): a, bipinnate neuroseta from segment 3; b, neuroseta from segment 4; c, neuroseta from segment 16; d, neuroseta from segment 29; e, harpoon notoseta from segment 5; f, acicular notoseta from segment 4; g, harpoon notoseta from segment 15; h, acicular notoseta from segment 16; i, harpoon notoseta from segment 29; j, acicular notoseta from segment 30; k, tip of harpoon showing sheath.

attached anterolaterally, last pair small, elongated with elytrophore attached laterally (Fig.40k-n).

First or tentacular segment with elongated uniramous parapodia, projecting anteriorly and laterally to prostomium, enlarged distally, forming rounded lobe, with tuft of fine capillary setae emerging medially and tuft of setae emerging posteriorly. Two pairs of tentacular cirri occurring dorsally and ventrally with large, cylindrical tentaculophores and styles long, subequal with slender, tapering, blunt tips, two-thirds length of median antenna.

Following segments with biramous parapodia. Second, third and fourth neuropodia with 2 tiers of neurosetae; lower tier with numerous (50+) golden yellow, bipinnate setae (Fig.40a); upper tier 2 neurosetae with basal spur and distal fringe (Fig.40b). Buccal cirri on segment 2 tapering, arising on base of neuropodia, swollen basally and extending to distal margin of neuropodia.

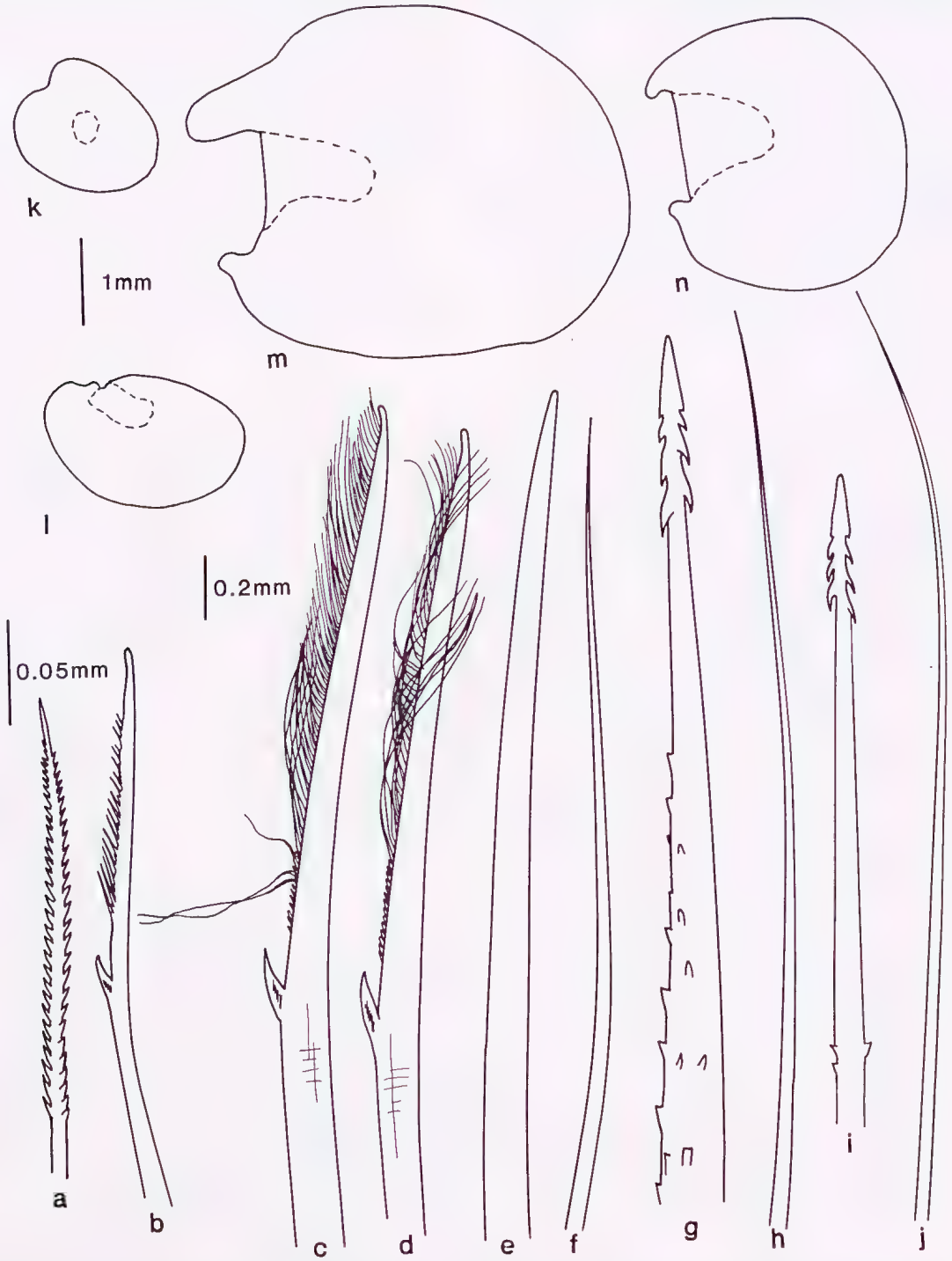

Fig.40. *Laetmonice malayana* (ZMA V.Pol 486.1): a, bipinnate neuroseta from segment 4; b, upper neuroseta from segment 4; c, neuroseta from segment 16; d, neuroseta from segment 25; e, smooth harpoon notoseta from segment 4; f, acicular notoseta from segment 5; g, harpoon notoseta from segment 16; h, acicular notoseta from segment 16; i, harpoon notoseta from segment 25; j, acicular notoseta from segment 25; k, first elytron; l, third elytron; m, eighth elytron; n, 14th elytron.

Remaining neuropodia elongate, smooth with 3-4 golden brown neurosetae with basal spur and distal fringe (Horst, 1917: pl.XIII fig.6). Ventral cirri swollen basally with tapering tips, not extending to distal tip of neuropodia.

Elytrigerous notopodia with tuft of about 10 golden brown, notosetal bristles (Fig.40f,h,j). Lateral to this tuft occurs tuft of 3-5 dark brown, thick harpoon notosetae, those on more posterior segments extending past posterior edge of body (Horst, 1917: pl.XIII fig.4). Harpoon notosetae pointing posteriorly, with 2-3 recurved fangs on lateral margins with shafts beset with a series of thorns (Horst, 1917: pl.XIII fig.5) (Fig.40g,i). Some anterior harpoon notosetae are smooth (Fig.40e). Ventral surface of notopodia with tuft of fine, pale yellow capillary notosetae.

Cirrigerous notopodia dorsal cirri with blunt tips one-third length harpoon notosetae, with tuft of golden brown, unidentate, mud-covered notosetae, harpoon notosetae lacking. Ventral surface of notopodia with short tuft of fine, pale yellow, unidentate notosetae.

Variations. In Table 7 we indicate the variation in numbers of different types of setae along the body on elytrigerous segments in four size classes. The numbers of neurosetae is constant over the body and with increasing size. In contrast the number of acicular notosetae is greatest on the middle segments and increases with increasing size and presumably age of the specimen. The number of harpoon notosetae varies slightly along the body with more occurring on anterior and middle segments and little evidence to demonstrate that numbers increase with increasing size of the individuals.

Remarks. We have considerably expanded Horst's original description, giving some indication of the variation existing within the species. The species has not been recorded since it was originally described.

The species is characterised by harpoon notosetae with shafts covered with a series of thorns which distinguishes it from other described species of *Laetmonice*, see Table 6.

Habitat. Trawled from depths of 798-959 m.

Distribution. Indonesian Archipelago (Fig.60).

Laetmonice moluccana (Horst)

Figs 41, 42a-f, 43a-j, 59E, 60, Table 7

Hermione moluccana Horst, 1916b: 70.–Horst, 1917: 52, pl.XII figs 6-10.
Hermonia moluccana Hartman, 1959: 56.

Type material examined. LECTOTYPE: Indonesian Archipelago Stn 138: east coast of Kajoa Island, 0°05'S 127°25'E (ZMA V.Pol 419.1), 2.3 cm long, 1.2 cm wide, 35 segments. PARALECTOTYPE: Indonesian Archipelago Stn 220: west coast of Binongka: Pasir Pandjang, 5°58'S 124°00'E (ZMA V.Pol 419.2), 2.5 cm long, 1.3 cm wide, 35 segments.

Additional material examined. Australia: NORTHERN TERRITORY: Port Essington, 11°04.5'S 132°05'E, 16 Sept. 1985, 8-9 m (NTM W3838), 2.5 cm long; Sandy Island, 11°05'S 132°16.5'E, 2 May 1982, 14 m (NTM W0206), 2.6 cm long; Darwin, 12°25'S 130°49.3'E, 3 Apr. 1986, 9 m (NTM W3928), 2.6 cm long; Channel Island, 12°33.3'S 130°52.4'E, 7 Dec. 1986 (NTM W4061), 0.42 cm long; Shell Island, 12°29.5'S 130°53.5'E, 2 July 1929, 6-13 m (LACM-AHF POLY 1301), 1.5 cm long, 0.5 cm wide, 32 segments; Mandora, 12°27'S 130°50'E, 22 Nov. 1972 AM W5438), 2.4 cm long; Mandora, 12°27'S 30°50'E, 20 Nov. 1972 (AM W5440), 3 cm long, 1.2 cm wide, 35 segments. WESTERN AUSTRALIA: Broome, 17°51'S 122°14'E, 25 Oct. 1972 (AM W5436), 2.8 cm long, 1.5 cm wide, 34 segments. QUEENSLAND: Capricorn Group, 23°30'S 152°00'E, May 1930 (USNM 148662), 2.9 cm long, 1.5 cm, wide, 32 segments; Heron Island, 23°27'S 151°55'E, 24 July 1975 (BMNH ZB 1990.27), 2.2 cm long, 1.2 cm wide, 32 segments.

Description. LECTOTYPE. Body elongate oval, 2.3 cm long, 1.2 cm wide. 35 segments.

Dorsum yellow coloured in alcohol, no felt covering elytra. Ventral surface creamy grey in alcohol, covered with spherical papillae (Fig.41).

Prostomium rounded with rounded ocular peduncles, one-third length of prostomium each with 2 contiguous

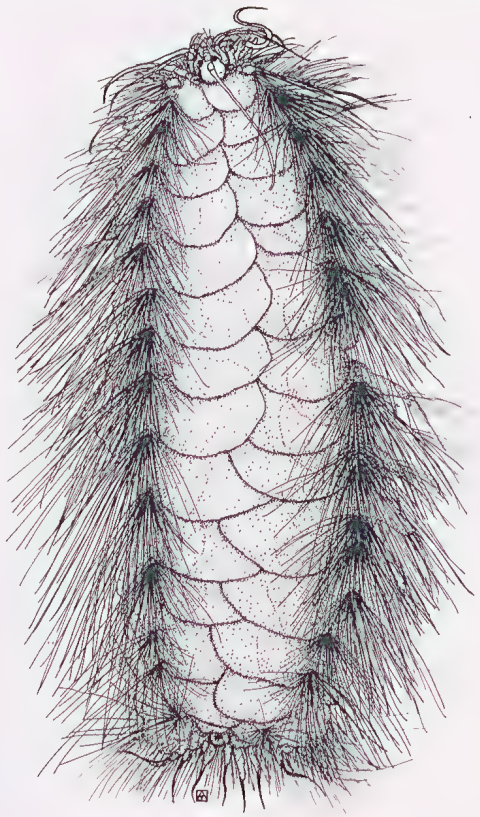

Fig.41. *Laetmonice moluccana* (AM W5440): dorsal view, whole animal.

dark grey eyes, dorsal one smaller, than larger ventral one. Median antenna with ceratophore 2-jointed, one third length of prostomium, style slender, clavate-tipped 5x length of prostomium. Palps extending to segment 6, margins finely papillated. Facial tubercle located below ceratophore visible ventrally, covered in small cylindrical papillae (Fig.42a).

Elytra 15 pairs, attached on elytrophores of segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28, then 31. Elytra thin, opaque, imbricating, first pair small, rounded with elytrophore attached in centre, following elytra large, ovoid with elytrophores attached laterally. All elytra covered in micropapillae (Fig.42c-f).

First or tentacular segment with elongated, uniramous parapodia, covered in large globular papillae, projecting anteriorly and laterally to prostomium. Dorsal surface of parapodia with tuft of golden yellow spines on inner distal edge, fanning towards prostomium. Two pairs of slender tentacular cirri on outer, distal edge of parapodia; dorsal pair three-quarters length of median antenna; ventral pair just shorter than dorsal pair. Ventral surface of parapodia with small tuft of fine, yellow setae.

Following segments with biramous parapodia. Second

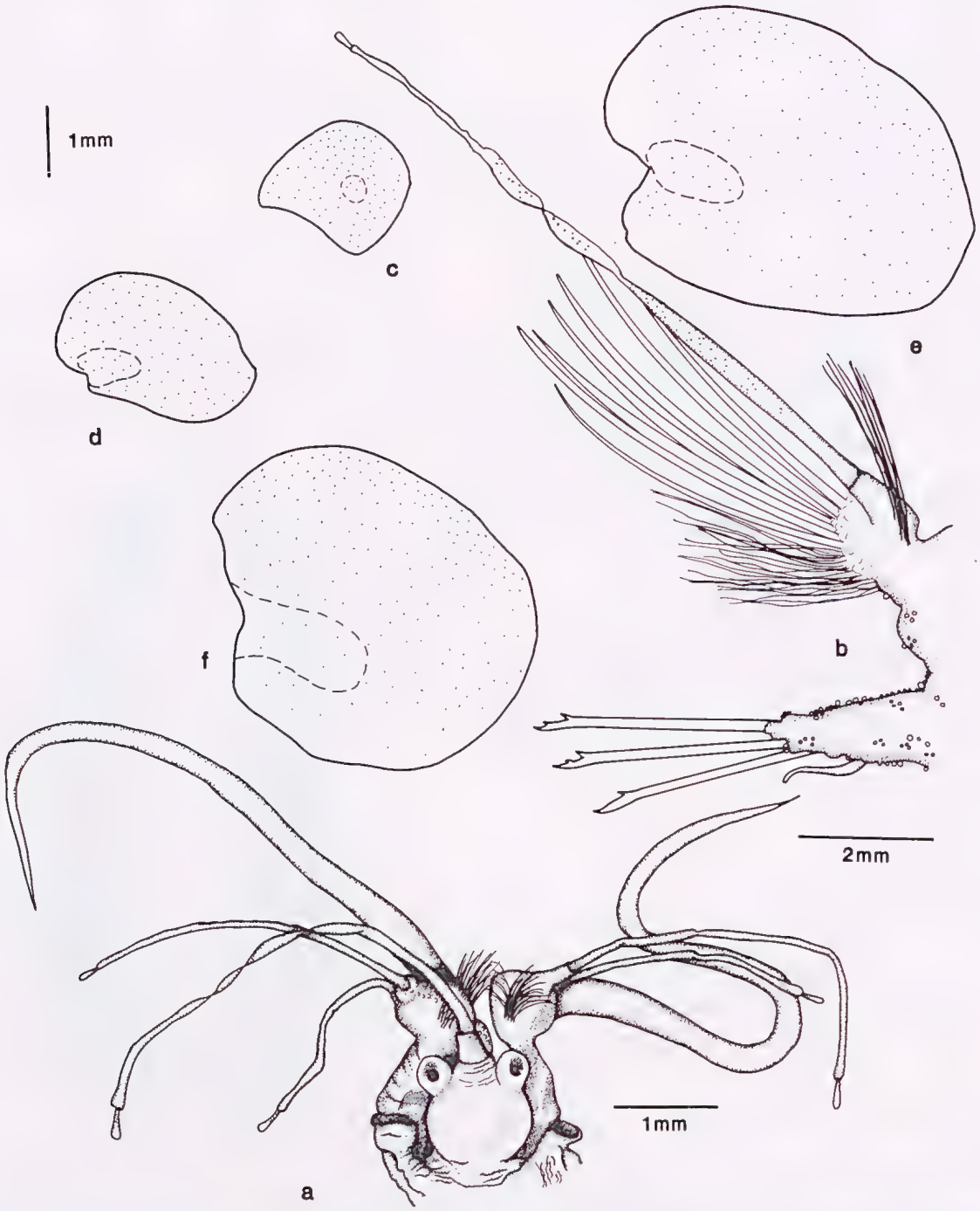

Fig.42. *Laetmonice moluccana* (AM W5436): a, dorsal view of prostomium and first segment; b, posterior view of parapodium 16; c, (AM W5432) first elytron; d, third elytron; e, eighth elytron; f, 14th elytron.

and third neuropodia with 2 tiers of neurosetae; lower tier with tuft of many (50+), golden yellow, bipinnate neurosetae (Fig.43a); upper tier with 2 golden yellow, neurosetae. Ventral cirri on second neuropodium arises from its base.

Remaining neuropodia elongate, covered with many large, rounded papillae, with 3-4 golden yellow neurosetae. Neurosetae with basal spur, slightly curved tip with 1-2 distal teeth (Fig.43c[1,2]). Neurosetae of anterior and posterior segments thinner, elongated (Fig.43b,d). Ventral cirri tapering to fine point, emerging below neurosetae extending to tip of neuropodia.

Elytrigerous notopodia with fan of smooth, yellow, acicular notosetae directed flat across elytra, completely covering dorsum (Fig.43e,h,j). Lateral to this fan occurring bundle of many harpoon notosetae, half body width, directed dorsally and slightly posteriorly, concealing dorsal surface. Harpoon notosetae with shafts smooth, tapering abruptly below tips with 3-4 recurved fangs on lateral margins forming darker harpoon tips, usually covered in clear sheaths (Fig.43f,g,i).

Cirrigerous notopodia with tuft of fine, short notosetal spines, directed dorsally and slightly posteriorly. Lateral to this tuft occurring fan of yellow, mud-covered notosetal spines fanning over neuropodia and covering neurosetae. Dorsal cirri with cirrophore emerging posterior to notosetae, styles long, slender, with clavate tips, equal to length of harpoon notosetae.

Variation. Additional material examined ranging from 0.42-3.0 cm long, 0.27-1.5 cm wide, 20-35 segments.

Remarks. *Laetmonice moluccana* is characterised by the elytra being completely covered by notosetae, and neurosetae with a basal spur and one to three distal teeth. These characters clearly distinguish it from all other species from the Indo-Pacific, see Table 6. For a discussion of the reasons why we have transferred this species to the genus *Laetmonice* see the Remarks section following the generic diagnosis of *Laetmonice*.

This is currently the only species of *Laetmonice* present in both the Indonesian Archipelago and northern Australian waters, and also the only Horst species which has subsequently been recorded since it was originally described.

Habitat. Found under rocks at low tide and also in muddy, shallow subtidal areas (6-14 m in depth).

Distribution. (Northern Australia from Broome, WA, 17°51'S 122°14'E to Capricorn Group, Qld, 23°30'S 152°00'E, Fig.59E). Indonesian Archipelago (Fig.60).

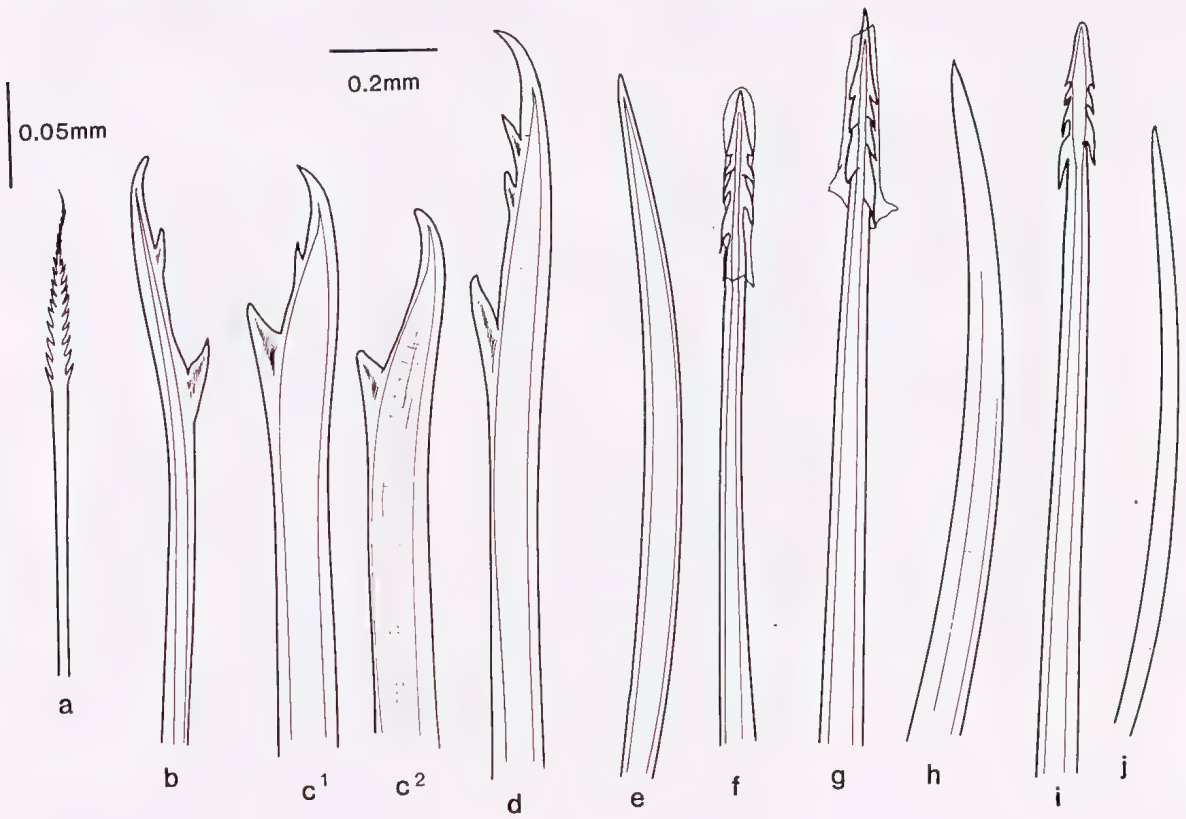

Fig.43. *Laetmonice moluccana* (AM W5432): a, bipinnate neuroseta from segment 4; b, upper neuroseta from segment 4; c[1,2], nuroseta from segment 16; d, neuroseta from segment 32; e, acicular notoseta from segment 4; f, harpoon notoseta from segment 5; g, harpoon notoseta from segment 16; h, acicular notoseta from segment 15; i, harpoon notoseta from segment 30; j, acicular notoseta from segment 31.

Laetmonice parva (Horst)

Figs 44a-g, 60, Table 6

Hermione parva Horst, 1916b: 70.–Horst, 1917: 53, pl.XII figs 14-16.
Hermonia parva Hartman, 1959: 56.

Type material examined. LECTOTYPE: Indonesian Archipelago Stn 65A: north off Tanah Djampeah, 7°05'S 120°42'E, 400 m (ZMA V.Pol 420), 1.5 cm long, 0.92 cm wide, 33 segments.

Description. Body elongate, oval, 1.5 cm long, 0.92 cm wide, 33 segments.

Dorsum tan, orange in alcohol, no felt covering elytra. Pharynx everted, large, without terminal papillae, terminal edge pilose. Ventral surface tan coloured, covered with spherical papillae.

Prostomium rounded with rounded ocular peduncles, half length of prostomium each with 2 faint grey eyes due to age, dorsal one smaller, than larger ventral one. Median antenna with ceratophore three-quarters length of prostomium, style slender, clavate-tipped 3 times length of prostomium. Palps extending to segment 7, margins finely papillated. Facial tubercle located below ceratophore visible ventrally, covered in cylindrical papillae.

Elytra 15 pairs, attached on elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra slightly opalescent, first pair small, triangular with rounded edges with elytrophore attached centrally, following elytra large, leaf-shaped, with elytrophore attached laterally, posterior elytra oval with elytrophore attached anterolaterally (Fig.44e-g).

First or tentacular segment with elongated uniramous parapodia, projecting anteriorly and laterally to prostomium, enlarged distally, forming rounded lobe, with tuft of short, fine setae, emerging radially from distal margins. Two pairs of tentacular cirri occurring dorsally and ventrally with, cylindrical tentaculophores and styles long, papillated, dorsal pair one and one-third times length median antenna, ventral pair half length of dorsal pair.

Following segments with biramous parapodia. Second, third and fourth neuropodia with 2 tiers of neurosetae; lower tier with tuft of many (100+), golden yellow, bipinnate neurosetae (Fig.44a); upper tier with 2 golden yellow, neurosetae with basal spur and 1-3 extra teeth (Fig.44b). Ventral cirri on second neuropodium arising from its base.

Remaining neuropodia elongate, cylindrical, papillated, with 2-3 golden yellow neurosetae. Neurosetae with basal spur and 1-2 extra teeth (Horst, 1917: pl.XII fig.16a,b). Ventral cirri slender, tapering, arising from middle of ventral surface of neuropodia, extending to distal margins of neuropodia.

Elytrigerous notopodia with dorsal fan of 6 or more golden yellow, unidentate notosetal spines, covered with

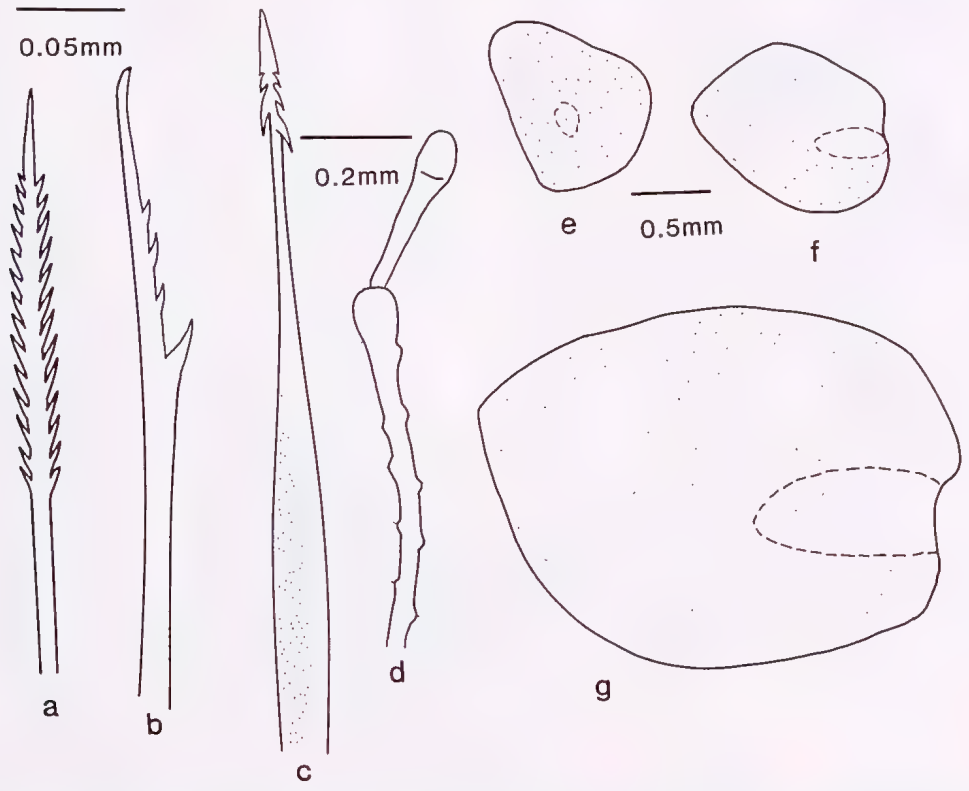

Fig.44. *Laetmonice parva* (ZMA V.Pol 420): a, bipinnate neuroseta from segment 3; b, upper neuroseta from segment 3; c, harpoon notoseta from middle segment; d, tip of dorsal cirri; e, first elytron; f, anterior elytron; g, middle elytron.

fine tubercles, pointing medially, lying flat across elytra. Lateral to this fan is tuft of about 13 long, golden brown, harpoon notosetae pointing dorsoposteriorly. Harpoon notosetae with shafts, covered in fine tubercles, tapering abruptly below tips with 2-3 recurved fangs on lateral margins forming harpoon tips, usually covered in clear sheaths (Horst, 1917: pl.XII fig.14), (Fig.44c).

Cirrigerous notopodia with fan of golden yellow, notosetal spines, directed medially and lying flat across dorsum. Lateral to this fan occurring tuft of about 25 longer, slightly curved, notosetal spines, beset with small papillae, directed posterolaterally (Horst, 1917: pl.XII fig.15). Dorsal cirri with large cylindrical cirrophores, styles long, tuberculated, slender, clavate tipped (Fig.44d).

Remarks. Pettibone (1966) synonymised the type species of *Hermione* Blainville 1828, *Halithea hystrix* Savigny in Lamarck, 1818 with *Laetmonice* Kinberg, 1856. This name was preoccupied and Hartman (1959) suggested the name *Hermonia* for this genus. For further comments see Remarks section after the generic diagnosis of *Laetmonice*.

Hermonia parva is also a species of *Laetmonice*, and we have considerably expanded the original description given by Horst (1916b, 1917). The species is known only from the type material.

The species is characterised by harpoon notosetae and notosetal spines with tuberculated shafts, and neurosetae with basal spur and one to three distal teeth, which distinguishes from other species of *Laetmonice* (see Table 6).

Habitat. Trawled at depths of 23 and 400 m.

Distribution. Indonesian Archipelago (Fig.60).

Laetmonice producta Grube

Figs 45a-f, 46a-j, 59E, Tables 6, 8, 9

Laetmonice producta Grube, 1878: 512-513.–McIntosh, 1885: 39-44, pl.VI fig.2, pl.IVa figs 1-8.–Horst, 1917: 54-56, pl.XIII figs 1-3.–Moore, 1903: 420.–Izuka, 1912: 82-84.

Material examined. TASMANIA: Sandy Cape, 41°25'S 144°45'E, 20 July 1987, 800 m, 9(AM W20235), 5.8-7.7 cm long; St Patricks Head, 41°35'S 148°14'E, 760-790 m, 3(AM W20233), 7 cm long; Maria Island, 42°44'S 148°01'E, Aug. 1921, 2377 m (AM W681), 8.2 cm; Southern Tasmania, 43°47.4'S 147°50.9'E, 20 Feb. 1976, 755 m (AM W9102), 5.4 cm long. VICTORIA: Gabo Island, 38°07.9'S 149°59.1'E, 14 Oct. 1984, 656-648 m, 2(NMV F56416), 7.1-7.8 cm long; Point Hicks, 38°16.4'S 149°27.6'E, 23 July 1986, 800 m, 2(NMV F56521), 7-7.8 cm long; Point Hicks, 38°21.9'S 149°20'E, 23 July 1986, 1000 m (NMV F56520), 5.6 cm long. NEW SOUTH WALES: off Nowra, 34°55'S 151°13'E, 12 Dec. 1978, 823 m, 68(AM W16563), 4-8.1 cm long; off Nowra, 34°54.68'S 151°11.36'E, 15 July 1986, 800-850 m, 11(NMV F56527), 2.4-6.6 cm long; south-east off Sydney, 34°24'S 151°25'E, 13 Dec. 1976, 731-768 m, 25(AM W16562), 4-6.6 cm long; off Bulli, 34°18'S 151°26'E, 29 May 1975, 457-476 m (AM W20230), 7.5 cm long; Broken Bay, 33°38'S 151°57'E, 2 Apr. 1975, 786-805 m, 16(AM W7254), 4-5.7 cm long; Broken Bay, 33°34'S 151°18'E, 731 m (AM W201612), 5 cm long; off Avoca, 33°41'S 152°00'E, 11 Feb. 1986, 819-889 m (AM W20232), 4.2 cm long; off Terrigal, 33°47'S 151°57'E, 7 Dec. 1978, 816 m, 63(AM W16564), 2.8-6 cm long.

HEARD ISLAND: 52°46.68'S 73°55.03'E, 19 June 1990, 3 m, (AM W20598).

Description. Body cigar shaped, 2.4-8.1 cm long, 1.2-3.5 cm wide, 41-45 segments.

Dorsum cream coloured in alcohol, with purple stripe running anteroposteriorly on dorsum. No felt covering elytra. Ventral surface cream coloured, covered in fine rounded papillae.

Prostomium rounded with 1 pair of large ocular peduncles, half length of prostomium without eye pigment. Median antenna with 2-jointed ceratophore half length of prostomium, with style slender, clavate-tipped antenna two and a half times length of prostomium. Palps with small basal palpophores, tapering and extending to segment 9-11, margins finely papillated. Facial tubercle located below ceratophore, covered in long conical papillae. Pair of prominent, free nuchal flaps, arising from posterior region of prostomium, variable in size (Fig.45a).

Elytra 18 pairs with firm stout attachments on elytrophores of segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28, 31, 34, 37 and 40. Elytra smooth, opaque, purple colouration on inner half, first pair small, triangular with rounded edges, with elytrophore attached in centre, following elytra large, ovoid, with elytrophore attached laterally, posterior elytra rounded with elytrophores attached laterally (Fig.45c-f).

First or tentacular segment with elongated, flattened, uniramous parapodia, projecting anteriorly and laterally to prostomium, with tuft of short, fine, stiff golden yellow bristles, fanning around distal margin of parapodia. Two pairs of long dorsal and ventral tentacular cirri with cylindrical tentaculophores and styles long, subequal with slender, tapering, bulbous tips, half length of palps.

Following segments with biramous parapodia (Fig.45b). Second, third and fourth neuropodia with 2 tiers of neurosetae; lower tier with numerous (100+) golden yellow, bipinnate neurosetae (Fig.46a); upper tier with 2 neurosetae with basal spur and distal fringe (Fig.46b). Ventral cirri on segments 2 and 3, slender, tapering, arising on base of neuropodia and extending past distal margins of neuropodia.

Remaining neuropodia elongate, cylindrical, with 3 golden yellow neurosetae. Neurosetae with basal spur and distal fringe (Fig.46c,d). Ventral cirri slender, tapering, arising from middle of ventral surface of neuropodia, extending below distal margins of neuropodia.

Elytrigerous notopodia with dorsal surface with tuft of about 15 or more golden yellow, acicular notosetae, varying in width. Lateral to this tuft occurs tuft of 10

or more, golden brown harpoon notosetae with tips darker (missing from most specimens), small tuft of pale yellow, unidentate notosetae anterior to harpoon notosetae. Harpoon notosetae length of body width, with shafts smooth, tapering abruptly below tips with 3-5 recurved fangs on lateral margins (Fig.46g). Some harpoon notosetae are smooth (Fig.46f). Ventral surface of notopodia with lateral-ventral tuft of short, fine, mud-covered capillary notosetae.

Cirrigerous notopodia with dorsal surface with tuft of about 20 golden yellow, smooth, acicular notosetae three-quarters length of harpoon notosetae (Fig.46e,h), anterior to this tuft, is tuft of fine, pale yellow, unidentate notosetae. Ventral surface of notopodia with tuft of fine mud-covered capillary notosetae. Cirrophore cylindrical, arising dorsolaterally on posterior side of notopodia, cirri long, thin, tapering with bulbous tips (Fig.45b).

Variation. Specimen NMV F56520 although externally appearing the same as other specimens from the same locality differs in possessing only 16 pairs of elytra, and in the arrangement and ornamentation of the elytra. Elytrigerous notopodia possess a fan of 16 or more harpoon notosetae with shafts densely tuberculated (Fig.46i,j), no acicular notosetae present. Cirrigerous

Fig.45. *Laetmonice producta* (AM W20235): a, dorsal view of prostomium and first segment; b, posterior view of parapodium 16; c, (NMV F56416) first elytron; d, third elytron; e, eighth elytron; f, 16th elytron.

notopodia with a fan of 20 or more densely tuberculated acicular notosetae.

The specimens from Heard Island differs in possessing pale elytra without the purple stripe, 20 pairs of elytra and much larger nuchal flaps present.

In Table 8, we give the number of different types of setae along the body in 4 size classes. The number of neurosetae present is constant along the body and is independent of the size of the animal. The number of acicular notosetae varies along the body and generally the greatest number is found on middle parapodia, although considerable variation occurs within a size class, but there is a general trend of numbers increasing with increasing size and presumably age. Harpoon notosetae show a similar pattern to that exhibited by the acicular notosetae.

Remarks. The stem species *Laetmonice producta* was originally described by Grube (1878), from Kerguelen Islands. Subsequently McIntosh (1885, 1900) described four varieties on the basis of general proportions of the prostomium and ocular peduncles, eye pigment, length of and ornamentation of the setae, and the amount of papillation of the ventrum (see Table 9).

McIntosh (1885:45) states that the "number of scales is however, of comparatively little moment, however we have however found them to be constant over a large size range with individuals as small as 2.4 cm possessing 18 pairs of elytra. Horst (1917) who identified four specimens as *L. producta* but refers to them as a variety, without giving the variety a name. He suggests that because *L. producta* has such a wide geographical distribution and is found at different depths, that it is not surprising that several varieties occur. We suggest that if these varieties were examined in detail these would be found to belong to separate species.

It may be that our variations belong to another species but as McIntosh's type material was not available for examination at this stage we prefer to refer our specimens to the stem species *L. producta*. A reappraisal of the validity of the varieties needs to be

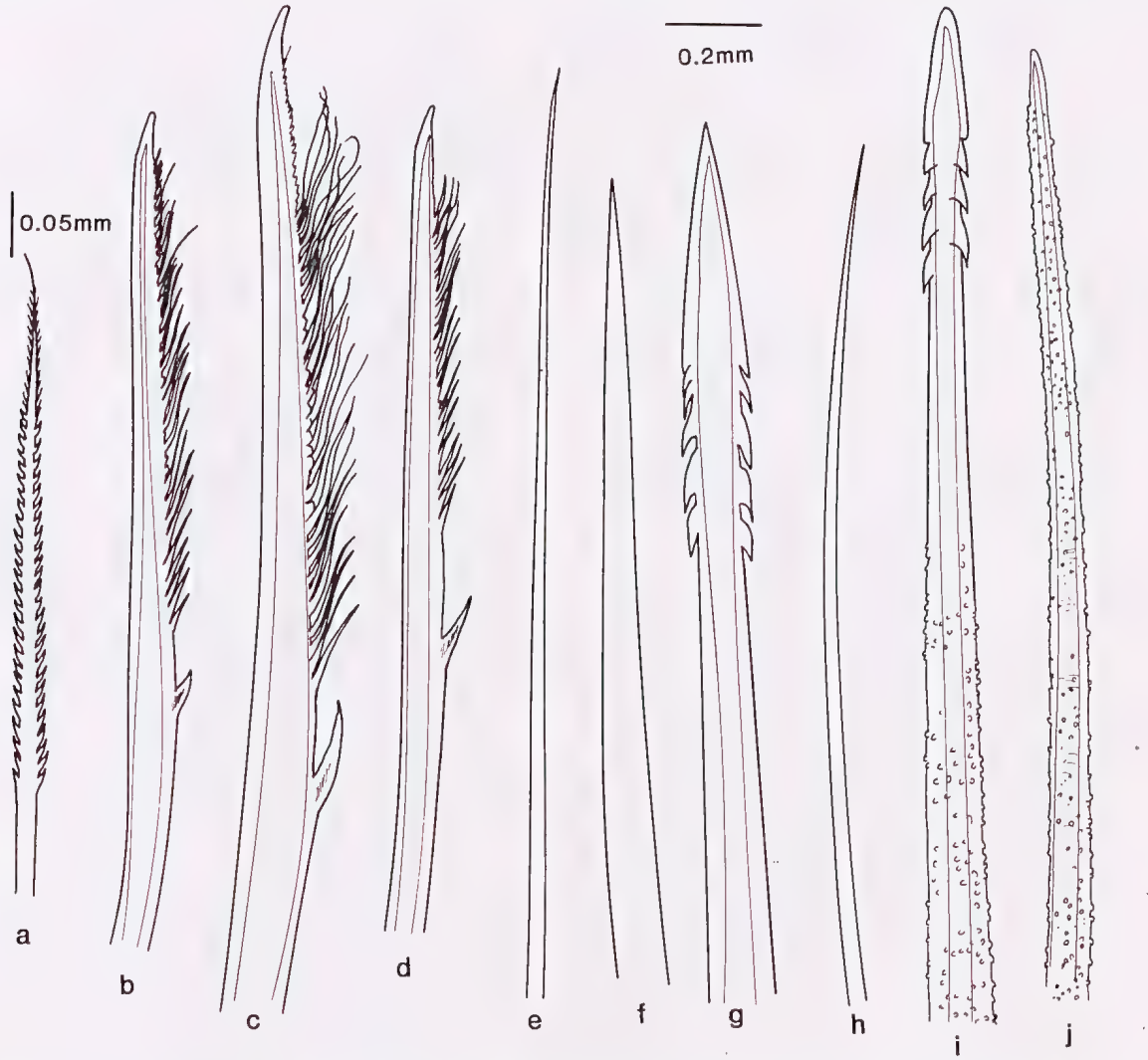

Fig.46. *Laetmonice producta* (AM W20235): a, bipinnate neuroseta from segment 3; b, neuroseta from segment 4; c, neuroseta from segment 16; d, neuroseta from segment 35; e, acicular notoseta from segment 5; f, smooth harpoon notoseta from segment 5; g, harpoon notoseta from segment 15; h, acicular notoseta from segment 15; i, (NMV F56320) harpoon notoseta middle segment; j, acicular notoseta middle segment.

undertaken, taking into account the consistency of elytral numbers and the geographical distributions, as two of McIntosh's varieties, *benthaliana* and *willemoesi* have extensive geographical distributions.

Habitat. Trawled at depths of 457-2377 m.

Distribution. Australia (South-east Australia from Sandy Cape, Tas., 41°25'S 144°45'E to Broken Bay, NSW, 33°34'S 151°18'E, Fig.59E).

Laetmonice rugosa Horst

Figs 47a-d, 60, Table 6

Laetmonice rugosa Horst, 1916b: 74.–Horst, 1917: 56-57, pl.XIII figs 7-9.

Type material examined. LECTOTYPE: Indonesian Archipelago Stn 302: north off Rotti Island, 10°27.9'S 123°28.7'E, 216 m (ZMA V.Pol 488.1), 3.6 cm long, 2.1 cm wide, 35 segments. PARALECTOTYPE: Indonesian Archipelago Stn 302: north off Rotti Island, 10°27.9'S 123°28.7'E, 216 m (ZMA V.Pol 488.2), 1.7 cm long, 1.1 cm wide, 32 segments.

Description. Body elongate oval, 1.7-3.6 cm long, 1.1-2.1 cm wide, 32-35 segments.

Dorsum cream coloured in alcohol, elytra covered with fine felt (damaged on lectotype). Ventral surface cream covered with many spherical papillae giving rugose appearance.

Prostomium rounded with 2 large ocular peduncles, without eye pigment, half length prostomium. Median antenna with 2-jointed ceratophore, styles now missing on both specimens. Horst (1917) states style long, clavate tipped, just shorter than palps. Palps, tapering, smooth, extending to segment 8. Facial tubercle small, situated below median antenna, visible only ventrally, covered in rounded papillae.

Elytra 15 pairs, attached on elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra thin, semi-transparent, slightly opalescent, first pair small, rounded with elytrophore attached centrally, following elytra large, leaf-shaped, with elytrophore attached laterally, posterior pairs small, rounded with elytrophore attached laterally. All elytra with some scattered micropapillae.

First or tentacular segment with elongated uniramous parapodia, projecting anteriorly and laterally to prostomium, enlarged distally, forming rounded lobe, with tuft of fine setae, emerging radially from medial to posterior margins. Two pairs of tentacular cirri with cylindrical tentaculophores and styles long, slender, clavate-tipped, dorsal pair 3 times length of prostomium, ventral pair three-quarters length of dorsal pair.

Following segments with biramous papapodia. Segments 2-4 with 2 tiers of neurosetae. Lower tier with tuft of many (20+) golden yellow bipinnate neurosetae (Fig.47a); upper tier with 2 golden yellow neurosetae with basal spur and 0-4 distal teeth.

Remaining neuropodia elongate, cylindrical, papillated with 2-4 golden yellow neurosetae with basal spur and 3-5 additional teeth (Horst, 1917: pl.XIII fig.8) (Fig.47b). Ventral cirri swollen basally with tapering tips, extending below distal margin of neuropodia.

Elytrigerous notopodia with dorsal fan of 10 or more golden brown, tuberculated, unidentate notosetal spines (Fig.47c). Lateral to this fan tuft of long, golden brown, harpoon notosetae pointing dorsoposteriorly, extending past posterior edge of body, with shafts smooth or with some fine tubercles, with 3 recurved fangs on lateral margins forming harpoon tips, many tips covered in transparent sheaths (Fig.47d).

Cirrigerous notopodia dorsal cirri with blunt tips, with tuft of golden brown, unidentate notosetal spines covered in fine papillae, pointing dorsolaterally, harpoon notosetae lacking. Ventral surface of notopodia with short tuft of fine, unidentate notosetae.

Remarks. We have considerably expanded Horst's descriptions (1916b, 1917) including indicating the numbers of different types of setae present. The species is known only from the type material. The species is characterised by having neurosetae with a basal spur and three to five distal teeth, and by having a ventral surface covered with many spherical papillae, these

Fig.47. *Laetmonice rugosa* (ZMA V.Pol 488.1): a, bipinnate neuroseta from segment 3; b, neuroseta from middle segment; c, acicular notoseta from middle segment; d, tip of harpoon notoseta from middle segment.

features distinguish it from other species of *Laetmonice*, see Table 6.

Habitat. Trawled at a depth of 216 m.

Distribution. Rotti Island, Indonesian Archipelago (Fig.60).

Laetmonice viridescens Horst

Figs 48a-c, 60, Table 6

Laetmonice viridescens Horst, 1917: 58-59, pl.XIV figs 1,2.

Type material examined. LECTOTYPE: Indonesian Archipelago Stn 137: channel between Makjan and Halmaheira, 0°23.8'N 127°29'E, 472 m (ZMA V.Pol 489.1); 1.9 cm long, 1.1 cm wide, 32 segments. PARALECTOTYPE: Indonesian Archipelago Stn 137: channel between Makjan and Halmaheira, 0°23.8'N 127°29'E, 472 m (ZMA V.Pol 489.2), 1.4 cm long, 0.9 cm wide, 31 segments.

Description. Body cigar shaped, 1.4-1.9 cm long, 0.9-1.1 cm wide, 31-32 segments.

Dorsum tan coloured in alcohol, with thin sandy felt covering elytra. Ventral surface cream, covered with minute spherical papillae.

Prostomium rounded with 2 large ocular peduncles, without eye pigment, half length prostomium. Median antenna with large ceratophore, three-quarters length prostomium, style long, slender, clavate-tipped, 6 times length prostomium. Palps long, tapering, finely papillated, extending to segment 12. Facial tubercle situated below median antenna, visible only ventrally, covered in small rounded papillae.

Elytra 14-15 pairs, attached to elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra transparent, faintly iridescent, meeting mid-dorsally, first pair small, rounded, elytrophore attached centrally, following elytra large, rounded, with elytrophore attached laterally, posterior pairs small, ovate with elytrophore attached laterally.

First or tentacular segment with elongated uniramous parapodia, projecting anteriorly and laterally to prostomium, enlarged distally, forming rounded lobe, with tuft of fine, mud-covered setae, emerging from medial to posterior margins. Two pairs of tentacular cirri with cylindrical tentaculophores and styles long, slender, clavate-tipped, dorsal pair half length of median antenna, ventral pair shorter than dorsal pair.

Following segments with biramous papapodia. Second, third and fourth neuropodia with 2 tiers of neurosetae. Lower tier consisting of numerous (20+) bipinnate neurosetae (Fig.48a); upper tier 2 neurosetae with basal spur and 10 extra teeth (Fig.48b) or with basal spur and distal fringe of short hairs, separated by an interval. Ventral cirri on segment 2-3, thin, tapering extending past distal tip of neuropodia; ventral cirri on segment 4 extending to distal tip of neuropodia.

Remaining neuropodia elongate, cylindrical, with 3 golden yellow neurosetae. Neurosetae with basal spur and distal fringe not separated by an interval (Horst, 1917: pl.XIV fig.2) (Fig.48c). Ventral cirri slender, tapering, arising from base of ventral surface of neuropodia, extending below distal margins of neuropodia.

Elytrigerous notopodia with dorsal tuft of about 5 fine, pale yellow, mud covered notosetae. Lateral to this tuft occurs tuft of about 7 long, golden brown, harpoon notosetae pointing dorsoposteriorly, with shafts tapering abruptly below tip with 3 recurved fangs on lateral margins forming dark brown harpoon tips (Horst, 1917: pl.XIV fig.1).

Cirrigerous notopodia with dorsal cirri long, thin, with tuft of long, pale yellow, unidentate, mud-covered notosetae pointing laterally, harpoon notosetae lacking. Ventral surface of notopodia with short tuft of fine, mud-covered, unidentate notosetae.

Remarks. We have considerably expanded the original description by Horst (1917), giving details of the number and structure of the various setal types present. The species is known only from the two specimens described by Horst.

The species is characterised by neurosetae with a basal spur adjacent to the distal fringe and can be distinguished from other species of *Laetmonice* using Table 6.

Habitat. Trawled at depths of 835 and 959 m.

Distribution. Indonesian Archipelago (Fig.60).

Fig.48. *Laetmonice viridescens* (ZMA V.Pol 489.1): a, bipinnate neuroseta from segment 3; b, upper neuroseta from segment 3; c, neuroseta from middle segment.

Laetmonice wonda n.sp.

Figs 49a-k, 59F, Table 6

Type material examined. HOLOTYPE: Australia: Western Australia: west-south-west of Lancelin, 31°04'S 113°50'E, 23 Mar. 1972, 256 m (WAM 134-72), 3.3 cm long, 1.7 cm wide, 35 segments. PARATYPES: Western Australia: west-south-west of Lancelin, 31°04'S 113°50'E, 23 Mar. 1972, 256 m (BMNH ZB 1990.28), 2 cm long, 1 cm wide, 34 segments; Lancelin, 31°04'S113°50'E, 23 Mar. 1972, 256 m (AM W20375), 2.5-3.5 cm long, 34 segments; Lancelin, 31°04'S113°50'E, 23 Mar. 1972, 256 m (WAM 107-90), 2.5-3.5 cm long, 34 segments; Beagle Island, 49°43'S 114°17'E, 20 Mar. 1972, 274-283 m (USNM 148663), 3.8 cm long, 1 cm wide, 34 segments.

Description. Body cigar shaped, 3.3 cm long, 1.7 cm wide, 35 segments.

Dorsum cream coloured in alcohol, no felt covering elytra. Ventral surface cream coloured, covered with small, spherical papillae.

Prostomium rounded with 2 small ocular peduncles, equal in length to one-quarter of prostomium each with dorsal and ventral pale grey eyes. Median antenna ceratophore 2-jointed, one-third length of prostomium style missing. Facial tubercle ranging from three-quarters length of prostomium to length of prostomium, covered in long tapering papillae. Palps with small palpophores, extending to 13th segment, long, tapering, margins finely papillated. Pair of prominent, free nuchal flaps arising from posterolateral region of prostomium

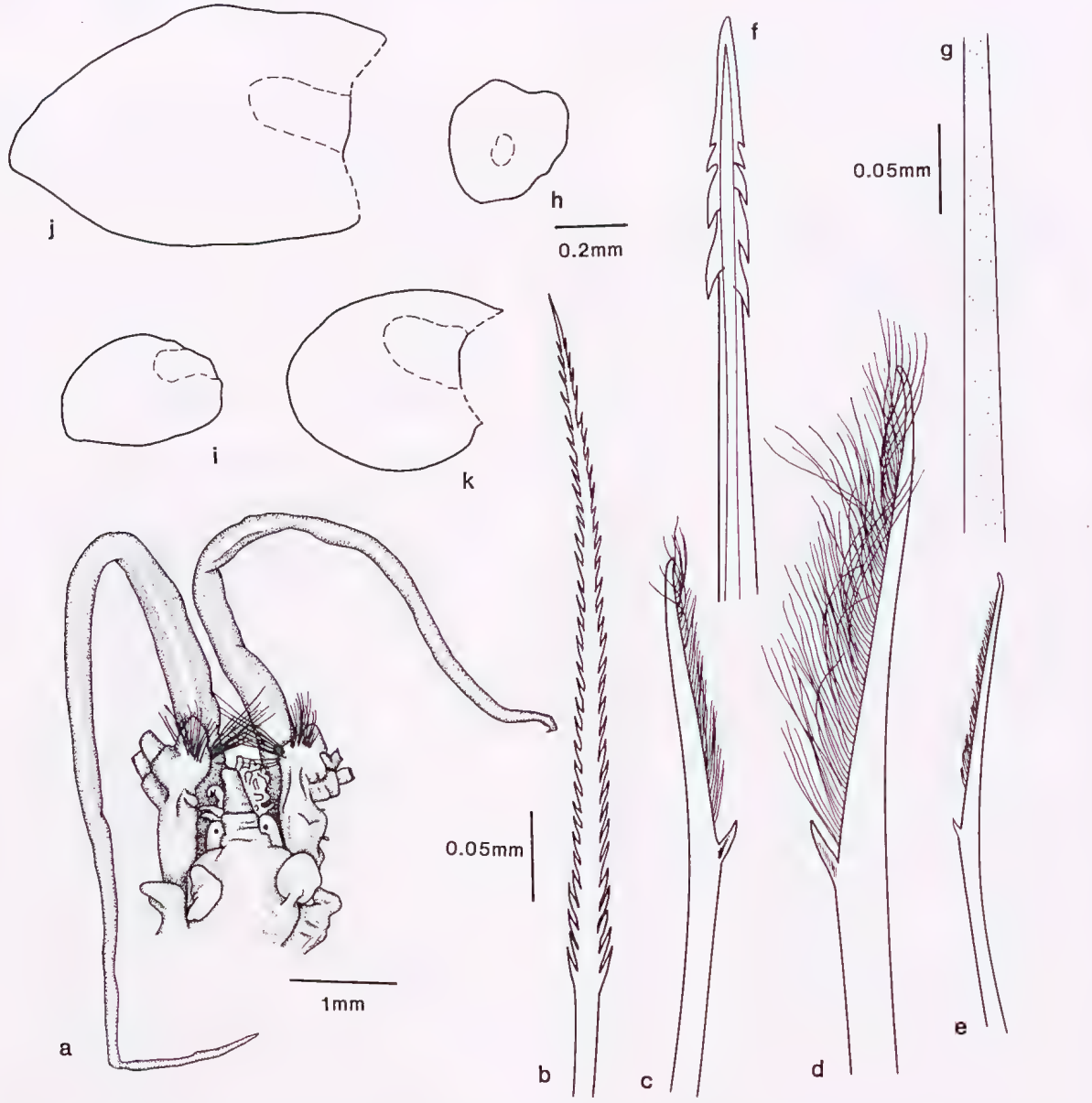

Fig.49. *Laetmonice wonda* n.sp. Holotype (WAM 134-72): a, dorsal view of prostomium and first segment; b, bipinnate neuroseta from segment 3; c, neuroseta from segment 4; d, neuroseta from segment 16; e, neuroseta from segment 32; f, tip of harpoon notoseta from middle segment; g, part of distal half of acicular notoseta from middle segment; h, (AM W20374) first elytron; i, third elytron; j, eighth elytron; k, 14th elytron.

(Fig.49a).

Elytra 15 pairs, attached to elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra imbricating, semi-transparent, smooth, cream coloured, first pair small, rounded attached to elytrophores in centre, following elytra larger, leaf-shaped, attached to elytrophores laterally, posterior elytra small, oval, attached to elytrophore laterally (Fig.49h-k).

First or tentacular segment with rectangular, elongated, uniramous parapodia, enlarged distally with short tuft of yellow setae on inner distal margins and longer tuft of setae on anterior end (Fig.49a).

Following segments with biramous parapodia, second, third and fourth neuropodia with 2 tiers of neurosetae; lower tier with tuft of numerous (100+) yellow, bipinnate neurosetae (Fig.49b); upper tier with 1-2 neurosetae with basal spur and fringe of hairs distally (Fig.49c). Ventral cirri on segment 2 slender, tapering, arising at base of neuropodia, extending past distal margins of neuropodia. Ventral cirri on segments 3 and 4 arising in middle of neuropodia, extending past distal margins of neuropodia.

Remaining neuropodia thin, cylindrical, elongate, with 3 golden yellow neurosetae, with basal spur and distal fringe of hairs (Fig.49d). Neurosetae of anterior and posterior segments with hairs of the fringe much shorter (Fig.49e). Ventral cirri slender, tapering, arising near base of neuropodia, extending to base of neurosetae.

Elytrigerous notopodia 3-13 with fan of 20 or more, fine, yellow, acicular notosetae with bases smooth and distal halves minutely tuberculated (Fig.49g) above elytrophore attachment and lateral tuft of 6-7 long harpoon notosetae, half body width, with shafts, thick, smooth, golden brown, tips small, dark brown, 3-4 recurved fangs on lateral margins of setae (Fig.49f). Elytrigerous notopodia 2-15, with fan of fine yellow, unidentate notosetal spines. First elytrigerous notopodia without notosetae.

Cirrigerous notopodia with tuft of long, fine, pale yellow, mud-covered notosetae on posterior surface of notopodia. Dorsal cirri with long, cylindrical, 2-jointed cirrophore on distal tip of notopodia, style missing. Ventral surface of notopodia with fan of short, yellow notosetae, directed laterally.

Variation. Additional material examined ranges from 2.4-4.1 cm long, 1.5-1.9 cm wide and 34-35 segments. Some harpoon notosetae beset with minute tubercles, occurring half way down shaft.

Remarks. *Laetmonice wonda* n.sp. is characterised by purse-like nuchal flaps on the prostomium, neurosetae with a fringe of hairs on the longer branch and harpoon notosetae which have shafts ornamented with tubercles. Only one other species of *Laetmonice* from the Indo-Pacific has purse-like flaps on the prostomium, *L. producta* Grube, but this species has smooth shafted harpoon notosetae in contrast to the tuberculated shafts present in *L. wonda* n.sp. This combination of characters present in *L. wonda* n.sp. clearly distinguishes it from all other described species of *Laetmonice* from the Indo-Pacific (see Table 6).

Habitat. Trawled at depths of 256-283 m.

Etymology. The specific name is from an aboriginal word *Wonda* meaning a shield, which refers to the shape of the new species.

Distribution. Australia (south-west Australia from Lancelin, WA, 31°04'S 113°50'E to Beagle Island, WA, 49°43'S 114°17'E, Fig.59F).

Laetmonice yarramba n.sp.

Figs 50a-e, 51a-h, 59F, Table 6

Type material examined. HOLOTYPE: Australia: New South Wales: Botany, 34°00'S 151°11'E, 60-102 m (AM W850), 1.8 cm long, 0.6 cm wide, 31 segments. PARATYPES: New South Wales: Botany Bay, 34°00'S 151°11'E, 60-102 m (USNM 148664), 1.7 cm long, 0.6 cm wide, 29 segments; Malabar, 33°58'S 151°15'E, Mar. 1974, 4(BMNH ZB1990.23-26), 1.8-2 cm long, 0.8-1.2 cm wide, 33 segments; Lake Macquarie, 33°05'S 151°40'E, 31 July 1959, 139-146 m, 4(LACM-AHF POLY 1300), 2.5-4 cm long, 0.8-1.5 cm wide, 34 segments.

Additional material examined. WESTERN AUSTRALIA: Shark Bay, 25°31'S 112°29'E, 9 Oct. 1963, 130 m, 4(WAM 24-75), 1.4-1.9 cm long. NEW SOUTH WALES: off Woy Woy, 33°29'S 152°06'E, 11 Feb. 1986, 492-523 m (AM W20231), 1.5 cm long.

Description. Body cigar shaped, 1.8 cm long, 0.6 cm wide, 31 segments.

Dorsal surface cream in alcohol. Ventral surface cream coloured, covered with small rounded papillae. Felt absent.

Prostomium rounded with ocular peduncles one-third length of prostomium without eye pigment. Median antenna with ceratophore half length of prostomium, style blunt tipped, 5 times length of prostomium. Palps extending to segment 9-11, margins very finely papillated. Facial tubercle located under ceratophore, visible only ventrally, covered with small cylindrical papillae. Prostomial nuchal flaps absent (Fig.50a).

Elytra 13-15 pairs, with elytrophores attached on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. Elytra cream coloured, opaque, smooth, first pair missing, following elytra larger, ovoid to leaf-shaped, attached to elytrophores laterally, posterior elytra small, triangular with rounded edges attached to elytrophore laterally (Fig.50c-e).

First or tentacular segment with elongated, flattened, uniramous parapodia, projecting anteriorly and laterally to prostomium, rectangular, flattened with short tuft of fine yellow setae on inner edge. Dorsal and ventral

tentacular cirri with tentaculophores on outer edge of parapodia, slender, tapering with blunt tips, one-third length of palps.

Following segments with biramous parapodia (Fig.50b). Second, third and fourth neuropodia with 2 tiers of neurosetae. Lower tier consisting of numerous (50+) yellow, bipinnate neurosetae (Fig.51a), upper tier with 2 yellow neurosetae with basal spur and distal fringe of hairs (Fig.51b,c). Ventral cirri with bulbous base, tips tapering to fine point, extending past distal tips of neuropodia.

Remaining neuropodia elongated, covered in small rounded papillae, with 3-4 golden yellow neurosetae, with basal spur and distal fringe of hairs (Fig.51d,e). Ventral cirri with bulbous base, arising in middle of neuropodia, not extending beyond ventral neurosetae.

Elytrigerous notopodia with tuft of stiff, yellow, smooth, mud-covered notosetae (Fig.51h), one-third length of harpoon notosetae. Lateral to this tuft, bundle of harpoon notosetae, as long as body width directed posterolaterally, with shafts smooth, tapering abruptly below tip with 3 recurved fangs on lateral margins (Fig.51f,g).

Cirrigerous notopodia with tuft of stiff, yellow, mud-covered notosetae on dorsal surface of notopodia, directed laterally and slightly posteriorly, as long as

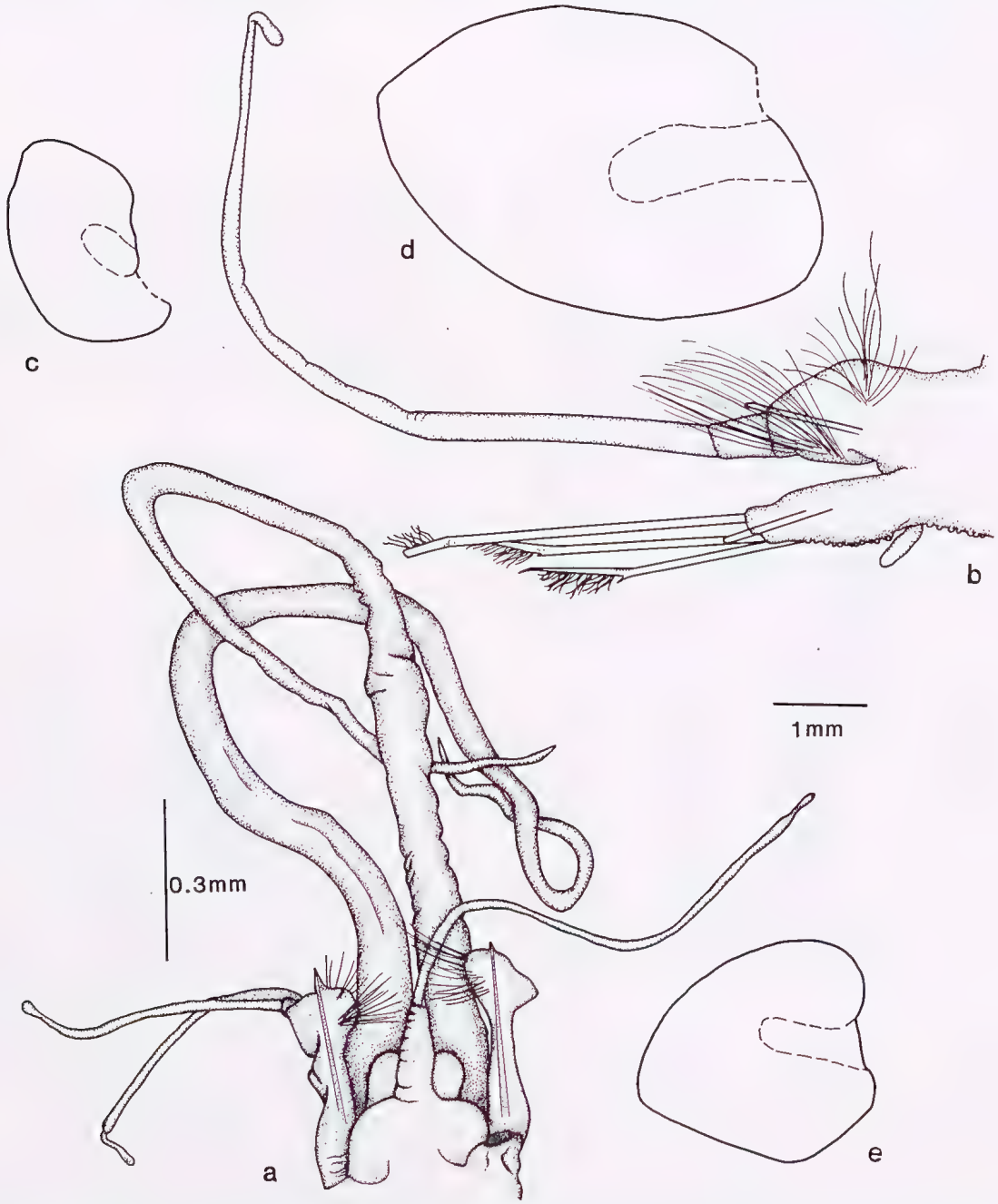

Fig.50. *Laetmonice yarramba* n.sp. Holotype (AM W850): a, dorsal view of prostomium and first segment; b, posterior view of parapodium 16; c, third elytron; d, eighth elytron; e, 14th elytron.

neuropodia. Ventral surface of notopodia with tuft of fine, mud-covered notosetae. Distal tip of neuropodia with cylindrical cirrophore, dorsal cirri posterior to notopodia and equal in length to harpoon notosetae, with blunt tips (Fig.50b).

Variation. Additional material examined ranges from 1.7-4 cm long, 0.6-1.5 cm wide, 29-34 segments. Some shafts of harpoon setae covered with small tubercles. Some specimens with transparent elytra and ventral surfaces without visible papillae.

Remarks. *Laetmonice yarramba* n.sp. is characterised by 13 to 15 pairs of elytra not covered in felt, finely papillated palps extending to ninth to 11th segment, three to four neurosetae with a fringe of hairs on the longer branch, harpoon notosetae with three recurved fangs, and some with tuberculated shafts (see Table 6). This combination of characters clearly distinguishes it from all other described species of *Laetmonice* from the Indo-Pacific.

Habitat. Trawled at depths of 60-523 m.

Etymology. The specific name is from an aboriginal word *Yarramba* meaning a shield, which refers to the shape of the new species.

Distribution. Australia (Shark Bay, WA, 28°31'S 112°29'E to Lake Macquarie, NSW, 33°05'S 151°40'E, Fig.59F).

Palmyra Savigny

Palmyra Savigny *in* Lamarck, 1818: 20.–Watson Russell, 1989: 40.
Palmyropsis Potts, 1910: 326 (fide Watson Russell, 1989: 40).

Diagnosis. Body broad, rectangular, with less than 40 segments. Thick epidermis with globular papillae. Prostomium with median antenna; 2 pairs of raised peduncles; 2 long palps; large facial tubercle. Segment 1 fused to prostomium with 2 pairs of tentacular cirri; short erect paleae fascicle, 2 fascicles of capillary notosetae. Large, flattened fascicles of broad paleae

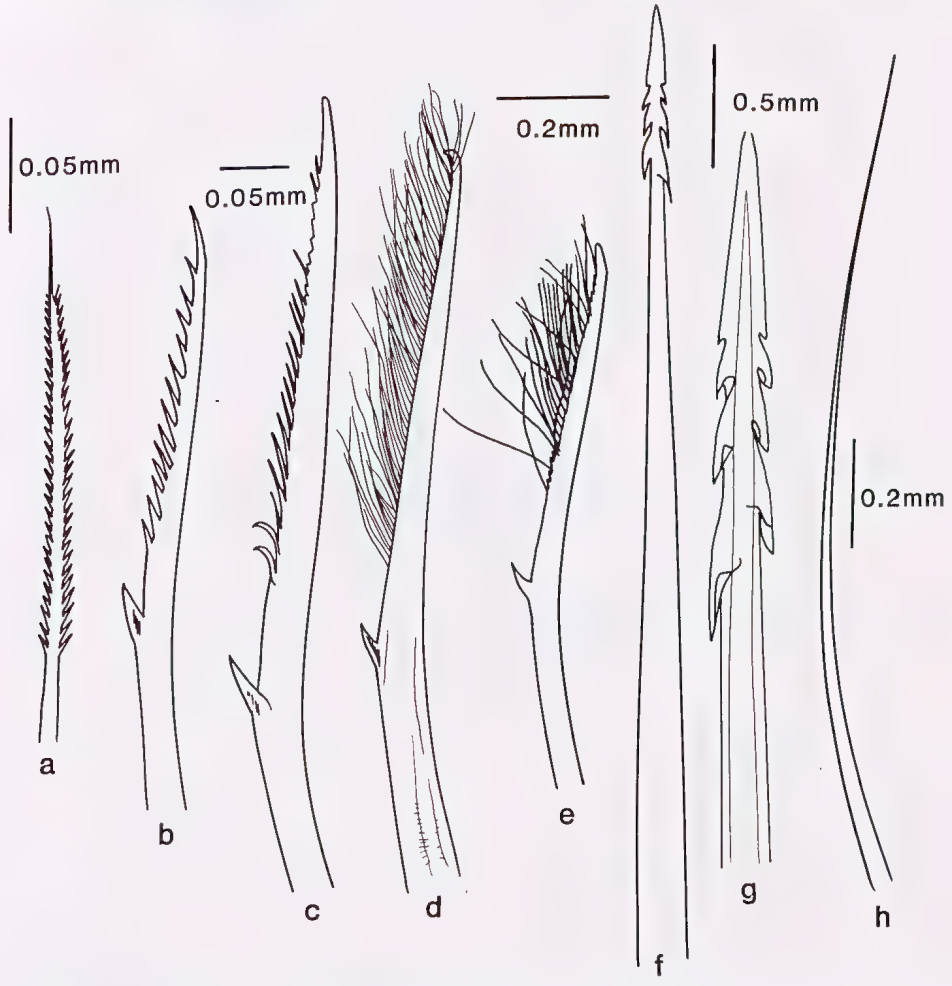

Fig.51. *Laetmonice yarramba* n.sp. Holotype (AM W850): a, bipinnate neuroseta from segment 3; b, upper neuroseta from segment 3; c, neuroseta from segment 4; d, neuroseta from segment 16; e, neuroseta from segment 25; f, harpoon notoseta from middle segment; g, tip of harpoon notoseta from middle segment; h, acicular notoseta from middle segment.

which imbricate down and across dorsum. Lateral small notopodial lobes with capillary setae. Paleal fans and dorsal cirri alternate. Neurosetae bipinnate and bidentate.

Type species. *Palmyra aurifera* Savigny, 1818, by monotypy.

Remarks. Watson Russell (1989) transferred this monospecific genus from the Chrysopetalidae to the Aphroditidae. She suggests that this genus is most closely related to *Pontogenia.*

Palmyra aurifera Savigny

Palmyra aurifera Savigny *in* Lamarck, 1818: 305.–Watson Russell, 1989: 44-51, pl.1a,b figs 1a-k, 2a-i, 3a-k, 4a-j, tables 1,2.

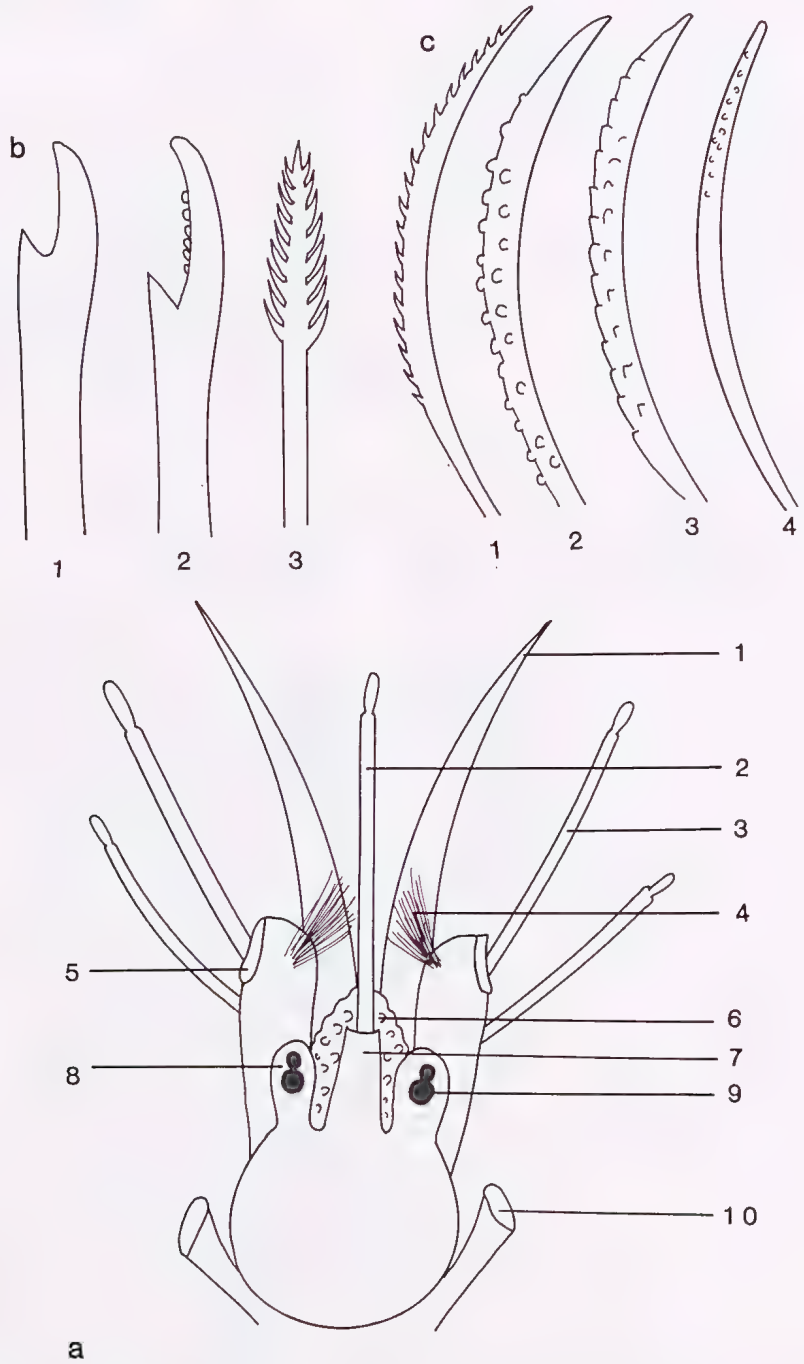

Fig.52. Generalised *Pontogenia.* a: dorsal view of prostomium and first segment – 1, palp; 2, median antenna; 3, tentacular cirrus; 4, setae; 5, tentaculophore; 6, facial tubercle; 7, ceratophore; 8, ommatophore; 9, eye; 10, elytrophore. b: neurosetal types – 1, bidentate; 2, bidentate with many small tubercles; 3, bipinnate. c: notosetal types – 1, paleal with long spines; 2, paleal, tuberculated; 3, paleal, serrated; 4, paleal, denticulated.

Material examined. None.

Remarks. Watson Russell (1989) has examined in detail the 13 Museum specimens known to exist of this species.

Habitat. Restricted to cracks and crevices in sponges, calcareous algae and corals.

Distribution. Western Indian Ocean, eastern Indian Ocean and Pacific Ocean (Watson Russell, 1989: fig.5).

Pontogenia Claparède

Pontogenia Claparède, 1868: 371-372.–Pettibone, 1966: 98.
Tricertia Haswell, 1883:274.
Pontogenessa Monro, 1924: 68-69.

Diagnosis. Aphroditids with dorsal felt poorly developed, not covering elytra completely. Elytra up to 18 pairs, smooth. Prostomium with club-like ocular peduncles. Facial tubercle well developed, papillated. Notosetae of 3 kinds: long, capillary setae; large flattened paleal setae arched over dorsum, serrated or papillated along margin; short capillary setae. Neurosetae stout, with slightly curved tips, smooth or with lateral spur.

Some neurosetae of anterior few segments bipinnate.

Type species. *Hermione chrysocoma* Baird, 1865, by monotypy.

Remarks. The above generic diagnosis is based upon Pettibone (1966), who synonymised *Pontogenessa* Monro, 1924 with *Pontogenia*. We have synonymised the monospecific genus *Tricertia* Haswell with *Pontogenia* as the type species of the genus *T. araeoceras* Haswell is clearly a species of *Pontogenia* as the notosetae are flattened and marginally serrated. In Figure 52 we figure a generalised *Pontogenia* and the types of setae present.

Key to the Indo-Pacific Species of *Pontogenia* *

1. Ceratophore longer than prostomium 2
—— Ceratophore shorter than prostomium 3
2. Paleal notosetae tuberculated (Fig.54e-g), about 23 present ..... *Pontogenia araeoceras*
—— Paleal notosetae with small denticles, about 14 present ..... *Pontogenia villosa*
3. Paleal notosetae about 10-25, denticulated giving serrated appearance (Fig.56e-g) ..... *Pontogenia macleari*
—— Paleal notosetae about 25 with long spines on each edge (Fig.57b) ..... *Pontogenia spinosa*

* We have not included *P. indica* Grube in the key as the original description is incomplete and we were not able to examine any material of this species.

Pontogenia araeoceras (Haswell)

Figs 53a-f, 54a-h, 59D, Table 10

Tricertia araeoceras Haswell, 1883: 274-275, pl.VIII figs 8-13, pl.VIII figs 1,2.

Type material examined. HOLOTYPE: Australia: Queensland: Port Molle, 20°20'S 148°51'E, Sept. 1908, 27.4 m (AM G11273), 2.5 cm long, 0.9 cm wide, 46 segments.

Additional material examined. WESTERN AUSTRALIA: Cathedral Rocks, 32°00'S 115°30'E, 15 Jan. 1991, 6 m (AM W20758), 1.5 cm long. QUEENSLAND: Outer Yonge Reef, 14°36'S 145°38'E, 15 Jan. 1977, 10 m (AM W20759), 1.6 mm.; Outer Yonge Reef, 14°36'S 145°38'E, 15 Jan. 1977, 2(AM W20757), 0.95-1.7 cm long; Outer Yonge Reef, 14°36'S 145°38'E, 15 Jan. 1977, 20 m, 2(AM W20756), 3.3-4.3 mm long.

Description. Body elongate oval, 0.16-2.5 cm long, 0.08-0.9 cm wide, 14-46 segments.

Dorsum cream coloured in alcohol, fine white felt notosetae covering elytra. Ventral surface cream, covered with many minute spherical papillae.

Prostomium rounded, 2 long ocular peduncles, half length of prostomium, 1 pair of grey eyes. Ceratophore, just longer than prostomium, median antenna with finely tapered articulate tip, one-quarter times longer than palps. Facial tubercle, papillated, located below ceratophore, visible only ventrally. Palps extending to sixth segment, margins covered in fine hairs (Fig.53a).

Elytra 15 pairs, attached on elytrophores of segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31. First pair of elytra oval with elytrophore attached laterally, remaining elytra large, oblong with rounded edges, convoluted on margins, elytrophores attached anteriolaterally (Fig.53b-e).

First or tentacular segment with elongated uniramous parapodia, with asymmetrical terminal lobe. Tuft of pale yellow, fine, unidentate setae emerge radially from distal margins of lobe. 2 pairs of cirri with finely tapered articulate tips, both arising from anterior tip of parapodia, dorsal pair three-quarters length of palps, ventral pair shorter than dorsal pair.

Following segments with biramous parapodia (Fig.53f). Second and third neuropodia squat, papillated, with 2 tiers of neurosetae; lower tier with small tuft of about 10 bipinnate neurosetae (Fig.54a); upper tier with 2-4 golden yellow, bidentate neurosetae with small tubercles on curved margins (Fig.54b).

Following segments with neuropodia stout, triangular, covered with small spherical papillae, with 3-4 golden yellow, stout, bidentate neurosetae (Fig.54c, d). Ventral

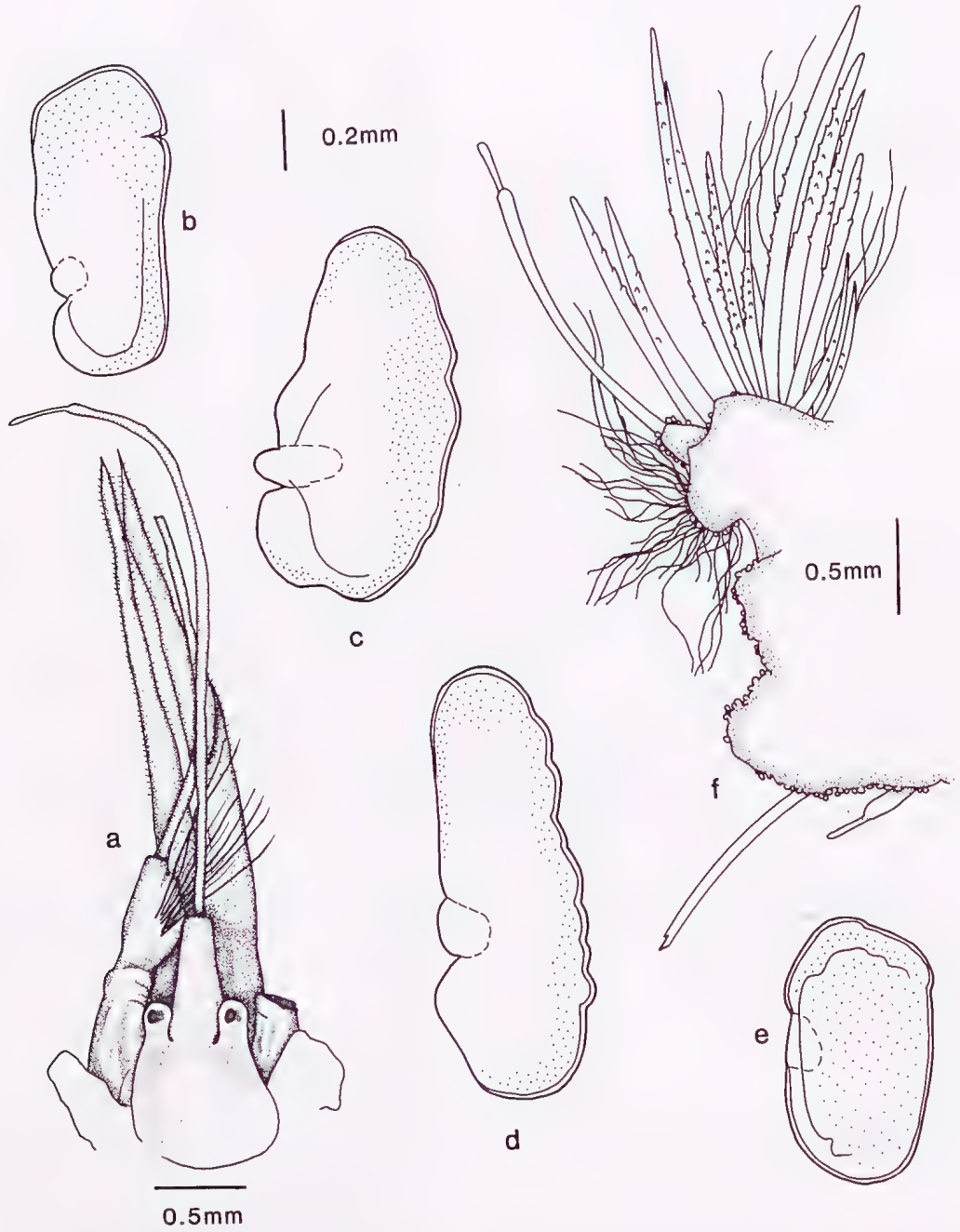

Fig.53. *Pontogenia araeoceras*. Holotype (AM G11273): a, dorsal view of prostomium and first segment; b, (AM W20757) third elytron; c, eighth elytron; d, 14th elytron; e, first elytron; f, posterior view of parapodium.

cirri with proximal region thick, distal region thin, extending to just below tip of neuropodia, except for ventral cirri on segment 2, which has long cirrophores, covered in cylindrical papillae, twice length of neuropodia. Notopodia stout with 2 kinds of notosetae, unidentate, mud-covered setae, and paleal setae arranged in 3 rows, fanning over dorsal surface of notopodia. Notosetal paleae golden brown, covered in minute tubercles (Fig.54e-h) arranged as follows; lateral group of 8 paleae which fan over neuropodia; 2 inner groups consisting of 6 and 9 paleae which fan over dorsum, almost touching mid-dorsally. Dorsal cirri with finely tapered articulate tips, length of paleal notosetae.

Variation. Ocular peduncles present on holotype only, the smaller remaining specimens with ocular peduncles fused to median ceratophore. Paleal notosetae on holotype large, cover the entire dorsum, smaller specimens with large paleal notosetae on anterior segments only, middle and posterior segments with small paleal notosetae, pointing medially, covered by felt.

Remarks. In his original description Haswell (1883) mentions the specimen having three tentacles emerging from the prostomium. However, the two outer tentacles are actually the dorsal cirri of the first tentacular segments. In Day & Hutchings (1979) the synonymy of *Tricertia araeoceras* with *P. araeoceras* was indicated by Kudenov, fide personal communication. Kudenov does not appear to have subsequently published this synonymy but we support his conclusions.

Pettibone's (1966) generic description of *Pontogenia* states that bipinnate neurosetae are absent on the anterior few segments. However, bipinnate neurosetae are present on the smaller specimens, the holotype was in a poor condition and bipinnate neurosetae were not observed.

Habitat. Found on dead coral substrate, coralline algae and reef limestone at depths of 10-27.4 m.

Distribution. Australia (Cathedral Rocks, WA, 32°00'S 115°30'E to Outer Yonge Reef, Qld, 14°36'S 145°38'E, Fig.59D).

Pontogenia macleari (Haswell)

Figs 55a-f, 56a-g, 59D, 60, Table 10

Hermione macleari Haswell, 1883: 273.
Hermonia macleari Hartman, 1959: 56.
Pontogenia nuda Horst, 1917: 62, pl.XIV figs 5-7.

Type material examined. HOLOTYPE: Australia: Queensland: Port Molle, 20°20'S 148°51'E, Sept. 1908, 25.6 m (AM G11272), 4.3 cm long, 1.1 cm wide, 39 segments.

Additional material examined. VICTORIA: Discovery Bay, 38°13'S 141°14'E, July 1969, 82-91 m (NMV F57188), 0.7 cm long. NEW SOUTH WALES: Balls Pyramid, 31°33'S 159°05'E, 22 Nov. 1960, 91-183 m (AM W20226), 0.9 cm long.

LECTOTYPE of *Pontogenia nuda*. Indonesian Archipelago: Stn 204: east of Buton Strait, 75-94 m (ZMA V.Pol 1189), 3.1 cm long, 1.1 cm wide, 37 segments.

NEW CALEDONIA: Kunie Island, 22°50'S 167°34'E, 8 May 1971, 274 m, 2(AM W20227), 1.6 cm long.

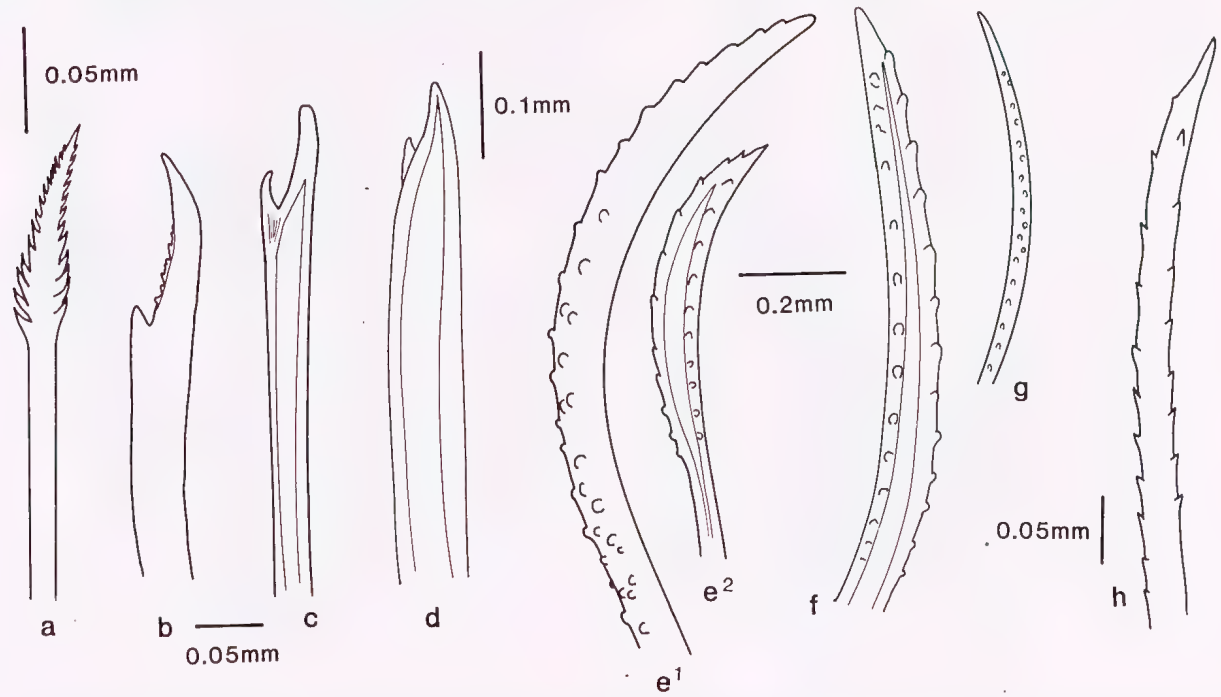

Fig.54. *Pontogenia araeoceras* (AM W20757): a, bipinnate neuroseta from segment 3; b, neuroseta from segment 4; c, neuroseta from segment 36; d, neuroseta from segment 16 (Holotype); $e^{1,2}$, notoseta from segment 4; f, notoseta from middle segment (Holotype); g, notoseta from segment 16; h, notoseta from segment 36.

Description. Body elongate oval, 0.9-4.3 cm long, 0.3-1 cm wide, 29-39 segments.

Dorsum covered in fine creamy grey felt covering elytra. Whole dorsum covered by golden brown notosetae. Ventral surface grey in alcohol, covered with many, small spherical papillae.

Prostomium small, rounded with two ocular peduncles, three-quarters length of prostomium, with one pair of large, dark grey eyes. Ceratophore just shorter than prostomium, median antenna (missing on holotype, but scar visible) 2 times length of prostomium with clavate tip. Palps extending to fifth segment, margins finely papillated. Facial tubercle covered in elongate papillae, equal to length of prostomium (Fig.55a).

Elytra 15 pairs, attached on elytrophores of segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 27 and

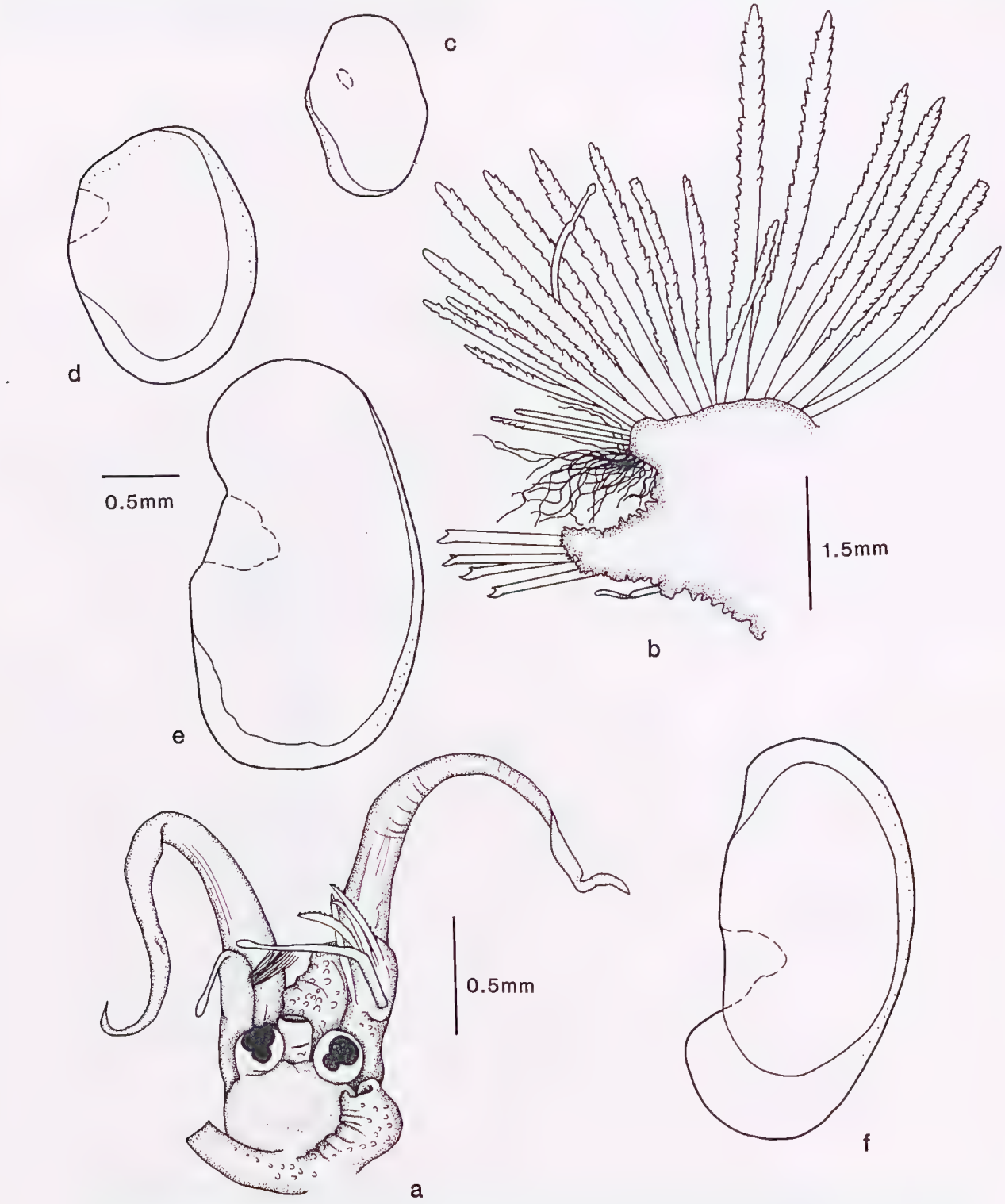

Fig.55. *Pontogenia macleari*. Holotype (AM W5436): a, dorsal view of prostomium and first segment; b, posterior view of parapodium; c, (AM W20226) first elytron; d, third elytron; e, eighth elytron; f, 14th elytron.

30. Elytra thickened medially with thin edges, first pair rounded with elytrophores attached centrally, following elytra large, oval with elytrophores attached laterally. All elytra with some scattered micropapillae (Fig.55c-f).

First or tentacular segment with elongated, uniramous parapodia, projecting anteriorly and laterally to prostomium. Inner distal edge of parapodia with fan of stiff, golden brown paleae. Two pairs of slender, clavate-tipped tentacular cirri on distal margins of parapodia, dorsal cirri, half length of palps, longer than ventral cirri. Posterior to ventral pair of tentacular cirri occurs tuft of short, fine, mud-covered setae (Fig.55a).

Following segments with biramous parapodia (Fig.55b). Second and third neuropodia squat, papillated, with 2 tiers of neurosetae; lower tier with small tuft of about 20 bipinnate neurosetae (Fig.56a); upper tier with 2-4 golden yellow, bidentate neurosetae. Large papillated cirrophore arises at base of neuropodia, ventral cirri clavate-tipped, 2 times length of neuropodia, except ventral cirri on 3rd neuropodia not extending to distal margin of neuropodia.

Remaining neuropodia stout, rectangular, densely papillated, with 2-4 golden yellow, stout, bidentate neurosetae (Fig.56b,c). Posterior neurosetae thinner, elongate (Fig.56d). Ventral cirri, clavate-tipped, not extending past distal tip of neuropodia (Fig.55b).

Remaining notopodia squat, with tuft of fine, mud-covered, capillary setae on ventral surface, length of neuropodia (not including neurosetae). Dorsal surface of notopodia with fan of 10-25, golden brown, notosetal paleae with denticles along each edge, giving serrated appearance, pointing posteriorly (Fig.55b, 56e-g). Tuft of fine, short, mud-covered, capillary notosetae arising from middle of each fan of paleae. Dorsal cirri with clavate tips, length of notosetal paleae (Fig.55b).

Variation. Ocular peduncles with two pairs of large grey, contiguous eyes, lateral pair larger on specimens from Balls Pyramid and one of the specimens from New Caledonia.

Remarks. The holotype is in poor condition, broken in two pieces, with fragile elytra, probably due to long term storage in alcohol. The description is therefore a composite one being based upon the holotype and other material examined.

Although Haswell (1883) originally described this species as belonging to *Hermione* Blainville, 1828, the

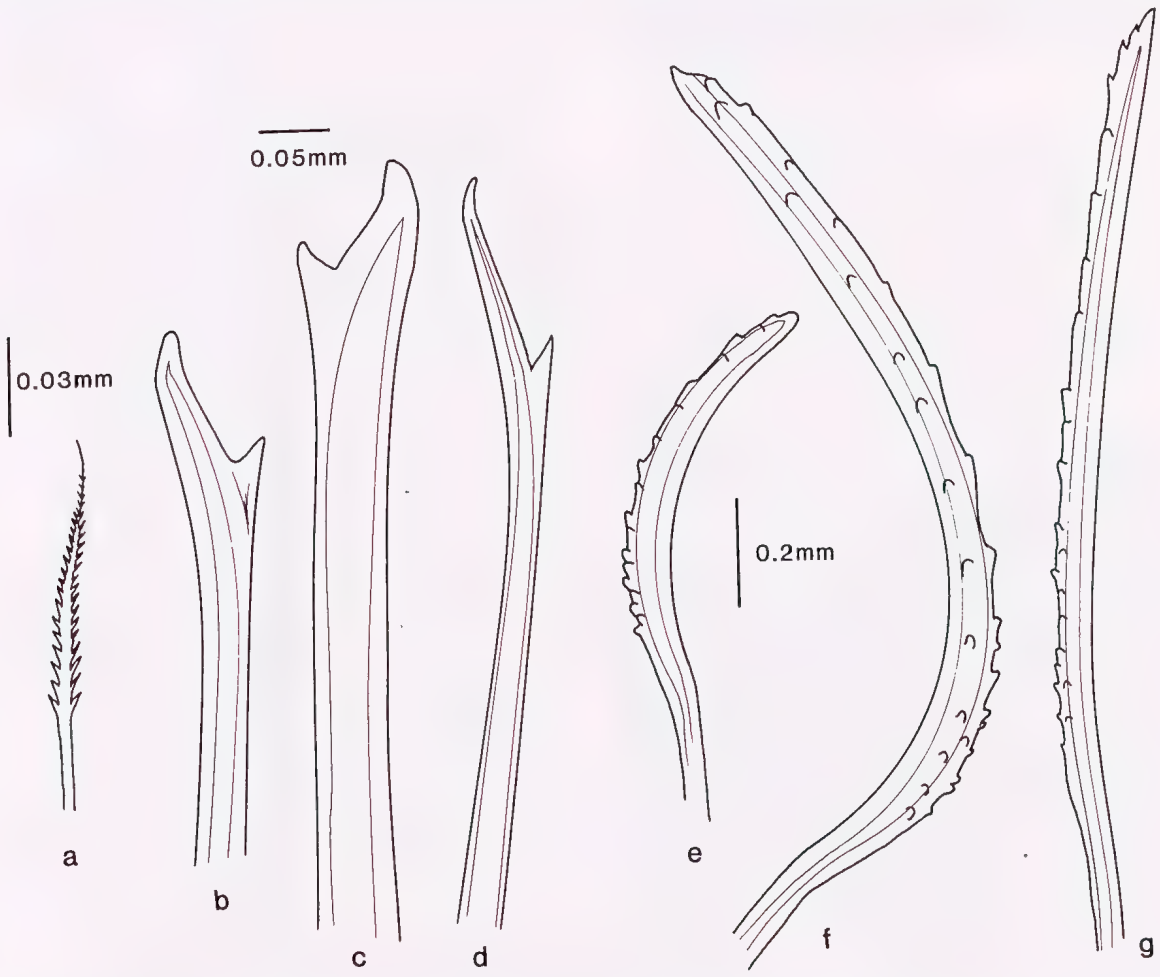

Fig.56. *Pontogenia macleari* (AM W20226): a, bipinnate neuroseta from segment 3; b, neuroseta from segment 4; c, neuroseta from segment 16; d, neuroseta from segment 30; e, notoseta from segment 4; f, notoseta from segment 16; g, notoseta from segment 30.

species clearly belongs in the genus *Pontogenia* Claparède, 1868; as harpoon notosetae are absent. The presence of such setae is diagnostic for *Laetmonice* Kinberg, 1856 (which incorporates *Hermionia*, see Pettibone, 1966 and comments on *Laetmonice* in this paper). Even though the type is in poor condition, it is certain that harpoon notosetae are completely lacking in the type specimen and we therefore have placed the species in the genus *Pontogenia*.

We have also synonymised *P. nuda* Horst, 1917 with *P. macleari* Haswell, 1883 as both type specimens are similar in all respects *Pontogenia nuda* Horst, 1917 was so called because of its lack of a dorsal felt, the holotype of *P. macleari* also lacks a dorsal felt, these specimens are both large individuals. The smaller specimens examined did possess a fine dorsal felt suggesting that the felt deteriorates with size and presumably age. In Table 10 we give the diagnostic characters of the Indo-Pacific species of *Pontogenia*.

Habitat. No habitat information given, found at depths of 25.6-274 m.

Distribution. Australia (Balls Pyramid, NSW, 31°33'S 159°05'E to Port Molle, Qld, 20°20'S 148°51'E, Fig.59D). New Caledonia; Indonesian Archipelago (Fig.60).

Pontogenia spinosa Horst

Figs 57a,b, 60, Table 10

Pontogenia spinosa Horst, 1917: 62-63, pl.XIV figs 8,9.

Type material examined. LECTOTYPE: Indonesian Archipelago Stn 154: Waigeu Island, 0°7.2'N 130°25.5'E, 83 m (ZMA V.Pol 1190), 2.5 cm long, 0.65 cm wide, 35 segments.

Description. Body elongate, oval, 2.5 cm long, 0.65 cm wide, 35 segments.

Dorsum cream coloured in alcohol, covered with felt. Ventral surface cream coloured, densely papillated.

Prostomium rounded with 2 large ocular peduncles, two-thirds length of prostomium, 2 pairs of dark grey eyes, anterior pair larger. Ceratophore cylindrical, covered in fine papillae, two-thirds length of prostomium, median antenna 3 times length of prostomium, clavate-tipped. Palps smooth, tapering, extending to segment 5. Facial tubercle situated below median ceratophore, therefore visible only ventrally, covered in elongate papillae.

Elytra 15 pairs, attached on elytrophores of segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 27 and 30. Elytra thin, semi-transparent, first pair rounded with elytrophore attached laterally, following elytra large, oval with elytrophores attached laterally, posterior elytra small elongate with elytrophores attached anterolaterally.

First or tentacular segment with uniramous parapodia, distal tip with tuft of mud-covered, fine capillary setae and short paleal setae. Two pairs of cylindrical tentaculophores covered in elongate papillae, styles clavate tipped, dorsal pair one-third length of median antenna, ventral cirri just shorter than dorsal cirri.

Following segments with biramous parapodia. Second and third neuropodia squat, papillated, with 2 tiers of neurosetae; lower tier with small tuft (20+) of bipinnate neurosetae (Fig.57a); upper tier with 2-3 neurosetae, all broken.

Remaining neuropodia stout, densely papillated, with 3-4 pale yellow, stout, bidentate neurosetae. Ventral cirri, clavate-tipped, extending to distal tip of neuropodia.

Remaining notopodia squat, with fan of fine, mud-covered, pale yellow capillary setae on ventral surface. Lateral edge with fan of 10 or more, short, pale yellow paleal notosetae, most broken. Dorsal surface of notopodia with 3 fans of about 25, golden yellow, notosetal paleae with long spines along each edge (Horst, 1917: pl.XIV fig.8) (Fig.57b), medial notosetae finer, fanning across dorsum, remaining pointing dorsoposteriorly. Dorsal cirri with clavate tips, length of notosetal paleae, emerging from posterior edge of notopodia.

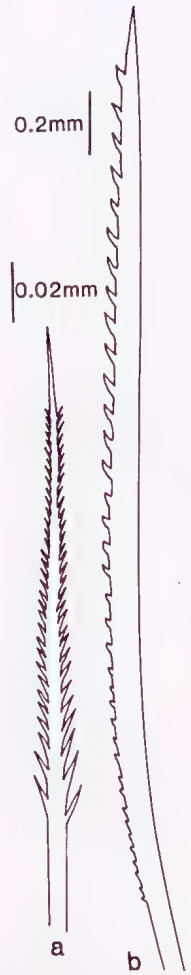

Fig.57. *Pontogenia spinosa* (ZMA V.Pol 1190): a, bipinnate neuroseta from segment 3; b, notoseta from middle segment.

Remarks. The species is known only from Horst's material, and the diagnostic features of this species are given in Table 10.

Habitat. Trawled at a depth of 83 m.

Distribution. Waigeu Island, Indonesian Archipelago (Fig.60).

Pontogenia villosa Horst

Figs 58, 60, Table 10

Pontogenia villosa Horst, 1917: 95, figs 1,2.–Monro, 1931: 3-4, fig.1a-c.

Type material examined. LECTOTYPE: Indonesian Archipelago Stn 131: Karakelang Islands: Beo, 4°14'N 126°47'S (ZMA V.Pol 1691), 2.4 cm long, 1 cm wide, 34 segments.

Description. Body elongate, oval, 2.4 cm long, 1 cm wide, 34 segments.

Dorsum tan coloured in alcohol, covered with thick felt obscuring paleal notosetae. Ventral surface tan coloured, finely papillated.

Prostomium partly hidden by segment 2, rounded with 2 large ocular peduncles, same length as prostomium, 2 pairs of dark grey eyes, ventral pair larger. Ceratophore cylindrical, covered in fine, elongate papillae, twice length of prostomium, median antenna same length as median ceratophore, but looks like it is broken. Facial tubercle small situated below median ceratophore, therefore visible only ventrally, covered in elongate papillae. Palps short, finely papillated.

First or tentacular segment with uniramous parapodia, removed from specimen, distal tip with tuft of fine, mud-covered, setae. Two pairs of cylindrical tentaculophores covered in elongate papillae, styles sub-equal in length, clavate-tipped with some small papillae.

Following segments with biramous parapodia. Neurosetae on segments 2-4 broken off, therefore presence or absence of bipinnate neurosetae cannot be determined.

Remaining neuropodia with 4 golden yellow, stout, bidentate neurosetae (Horst, 1917: fig.2). Ventral cirri, clavate-tipped, not extending to distal tip of neuropodia.

Remaining notopodia with dorsal surface with fan of about 14 golden yellow, slightly curved notosetal paleae with small denticles (Horst, 1917: fig.1) (Fig.58), also long felt notosetae, some jointed. Ventral surface of notopodia with tuft of fine, unidentate, mud-covered notosetae also mud-covered capillary notosetae. Dorsal cirri with elongate cylindrical cirrophores with small papillae, styles with clavate tips, shorter than notosetal paleae.

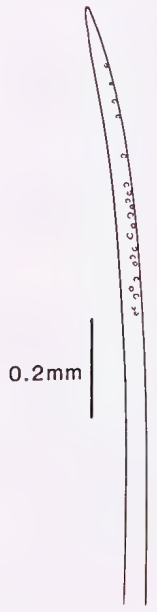

Fig.58. *Pontogenia villosa* (ZMA V.Pol 1691): notoseta from middle segment.

Remarks. Specimen gravid indicating mature size. Elytra were not described as only one specimen was available for examination with the dorsal felt still intact. The main diagnostic characters of this species, which is only known from Horst's material are given in Table 10.

Habitat. Trawled, depth not recorded.

Distribution. Karakelang Islands, Indonesian Archipelago (Fig.60).

Discussion

While this study of Australian aphroditids has revealed several new species together with new records of species previously known only from the original record, one Australian species is only known from the single original record, *Aphrodita terraereginae* Haswell. This is probably a reflection of the lack of collecting from offshore areas in Australia rather than their limited distribution. We also anticipate that additional species are present in Australian waters.

Of the 18 species of Aphroditidae presently recorded from Australian waters, only five are known to occur outside Australian waters. We anticipate this will change with increased collecting in the Indo-Pacific region. Of these five species, four occur in the Indonesian Archipelago and one occurs in New Zealand waters. The remaining 16 species are currently known only from the original type material collected in the Indonesian Archipelago. As many of these species occur in deep water, one might have expected more species to occur in both the Indonesian Archipelago and Northern Australia, and this perhaps is

a reflection of the limited collecting carried out offshore in northern Australia.

Currently the Australian species exhibit three major geographical patterns, species with extensive geographical ranges such as *A. australis* Baird and *A. goolmarris* n.sp., and those with a restricted distribution such as *L. dolichoceras* (Haswell) and *L. wonda* n.sp. and those which are currently known only from one locality, *A. malkaris* n.sp. Unfortunately, no recent survey of aphroditids has occurred elsewhere, so we cannot put our study into a broader biogeographical context. Although the family Terebellidae, which is well represented in Australian waters both at depth and in shallow waters exhibits similar patterns (Hutchings & Glasby, 1991).

Our study has also highlighted the need for generic revisions within this family, all the genera were described in the late 1800s and early 1900s as aphroditids are typically large and conspicuous. The type species of the genera need to be re-examined and we suspect that several undescribed genera are present within the family.

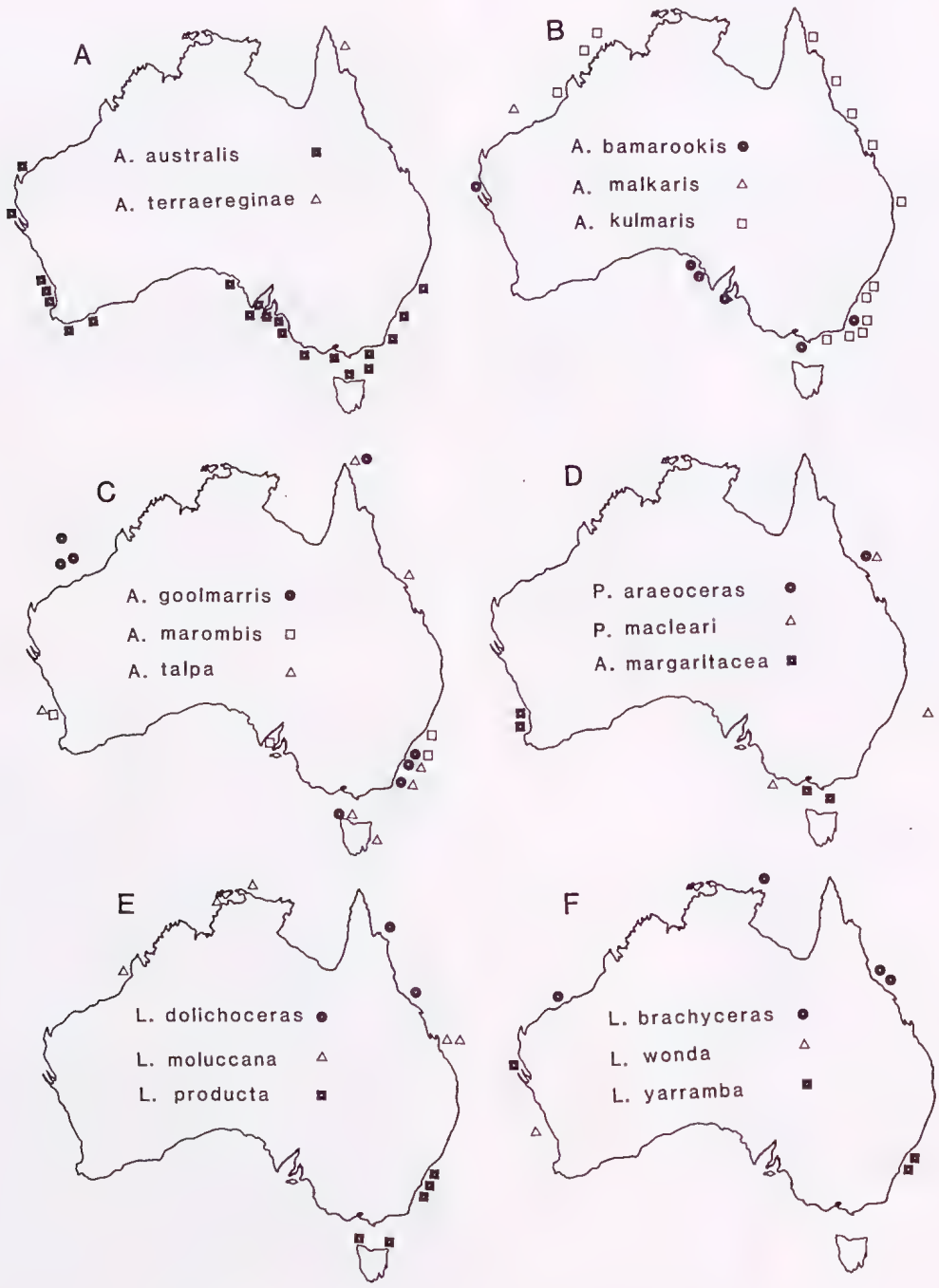

Fig.59. The Australian distribution of A-C, *Aphrodita* spp; D, *Pontogenia* spp and *Aphrogenia* spp; E, F, *Laetmonice* spp.

Fig.60. Indonesian Archipelago showing type localities of Horst's Siboga material of family Aphroditidae: A.d. = *Aphrodita decipiens*, A.f. = *Aphrodita floresiana*, A.l. = *Aphrodita limosa*, A.m. = *Aphrodita malayana*, A.n. = *Aphrogenia nigropunctata*, A.v. = *Aphrogenia villosa*, L.a. = *Laetmonice arenifera*, L.b. = *Laetmonice batheia*, L.br. = *Laetmonice brachyceras*, L.c. = *Laetmonice conchifera*, L.m. = *Laetmonice malayana*, L.mol. = *Laetmonice moluccana*, L.p. = *Laetmonice parva*, L.r. = *Laetmonice rugosa*, L.v. = *Laetmonice viridescens*, P.n. = *Pontogenia nuda*, P.s. = *Pontogenia spinosa*, P.v. = *Pontogenia villosa*.

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Table 1. Distinguishing characters of Australian and Indo-Pacific species of *Aphrodita*.

Species name	Length (cm)	No. of segments	Eyes	Median antenna	Palps (extending to setiger no.)	Facial tubercle	Notosetae	Lateral Fringe	Neurosetae	No. of Neurosetae	Distribution
Aphrodita australis Baird, 1865	1.4-19	41-45	1-2 pairs, large contiguous	small spherical papilla	5-8 finely papillated	3/4 to length of prostomium	smooth, thick, golden brown	long, iridescent green	smooth with slightly curved tips	7-8	Australia Japan* New Zealand*
Aphrodita bamarookis n.sp.	3-6	49-52	1 pair, small, grey	small papilla	4-6 smooth	length of prostomium	fine, slightly iridescent	long iridescent, cream/pink	smooth subulate	24-27	Southern Australia
Aphrodita decipiens (Horst, 1916b)	1-2	35	2 pairs raised, ocular area	1 slender length prostomium	6-7 finely papillated	length prostomium	golden brown, covered in tubercles with fine hooked hairs, tip	short mud covered	slightly curved with plumose edge	7-8	Indonesian Archipelago
Aphrodita floresiana Horst, 1916b	0.8-2.7	28-34	2 pairs, small raised ocular area	small ceratophore style thin, 3/4 length prostomium	6-7 finely papillated	length of prostomium	stout, short, covered in tubercles bent, slightly hooked tips	short mud covered	slightly curved with plumose edge	11-16	Indonesian Archipelago
Aphrodita goolmarris n.sp.	2.6-6	35-41	absent, raised ocular area	rod-shaped, 1/5 prostomium	7-11 smooth or finely papillated	length of prostomium	stout, golden brown	short, faintly iridescent	pilose tipped	14-26	Australia
Aphrodita japonica Marenzeller, 1879	4.7-15.1	36-42	2 pairs, small slightly raised	1 1/3 x length of prostomium	* 4 length prostomium, finely papillated	shorter than prostomium	smooth, thick entangled in felt	iridescent reddish	slightly curved tips	16-21	Southern Japan'
Aphrodita kulmaris n.sp.	1.8-10	38-46	2 pairs, grey	small papilla	5-7 papillated	1-2x length prostomium	stout, golden brown, smooth	long, iridescent red/green	some pilose tipped	21-29	Eastern and western Australia
Aphrodita limosa (Horst, 1916b)	2.7	36	absent raised ocular area	thin 3/4 length of prostomium	finely papillated 7	length of prostomium	smooth bases distal regions with fine tubercles and hairs hooked tips, entangled in felt	short mud covered	slightly curved tips with plumose edge	11-12	Indonesian Archipelago

Table 1 (cont'd).

Aphrodita malayana (Horst, 1916b)	3.5-3.7	32-38	absent raised ocular area	slender just longer than prostomium	6, finely papillated	length of prostomium	long, stout, dark brown, finely tuberculated	cream mud covered shorter than neurosetae	slightly curved tips with plumose edge	8	Indonesian Archipelago
Aphrodita malkaris n.sp.	2.7-3	33-35	absent, raised ocular area	bulbous, 1/3 prostomium	7 smooth	shorter than prostomium	long with triangular tips	short, faintly iridescent	sligthly curved ends, extra teeth or plumose edge	12-13	Western Australia
Aphrodita maorica Benham, 1900	6.3	?	?	?	?	?	long, bronze	short yellow mud covered	stout, brown	15	New Zealand'
Aphrodita marombis n.sp.	1.3-2.8	32-36	2 pairs, slightly raised ocular area	small papilla 1/3 length prostomium	4-5 finely papillated	length of prostomium	stout, covered in small tubercles	short, mud-covered	smooth with slightly curved tips	6-9	Southern Australia
Aphrodita sibogae (Horst, 1916b)	2.2	?	2 pairs raised ocular area	thin, just shorter than prostomium	smooth 5x length prostomium	3/4 length of prostomium	slender	?	slightly curved tips with plumose edge	?	Indonesian Archipelago'
Aphrodita sondaica Grube, 1875	8.0	39	1 pair, pale	blunt, tipped, 1/3 length prostomium	*3x length prostomium	?	stout, in fan shape, entangled in felt	iridescent mud covered	smooth, slightly curved tips	9-11 inferior tier	North Borneo'
Aphrodita talpa Quatrefages, 1866	0.7-4.5	31-38 40* (Monro)	2 pairs, small black	elongate, slightly enlarged tip, length of prostomium	3-5 smooth	3/4 length of prostomium	smooth entangled in felt	short faintly iridescent	slightly curved tips with plumose edge	10-15	Australia New Zealand
Aphrodita terraereginae Haswell, 1883	2.5	40	1 pair, large, grey, slightly raised	small, rod shaped	7 finely papillated	1/3 length prostomium	thick, paleal like, smooth pale yellow	short faintly iridescent	slightly curved tips inconspicous	8-10	Northern Australia
Aphrodita watasei Izuka, 1912	5.5-7	34-38	absent	long slender	* 5x length median antenna	short	stout, entangled in felt	short mud covered	smooth, curved tips	20	Japan'

* Original description does not indicate the setiger number to which palps extend, only length in relation to prostomium or median antenna.

' Indicates that these geographical records have not been checked by examination of material.

Table 2. Numbers of neurosetae present in different size classes of *Aphrodita australis*.

Length cm	Segment number	Lower tier (no. setae)	Middle tier (no. setae)	Upper tier (no. setae)
1-3	4	3	2	2
(n=4)	15	3-6	2-4	2
	25	2-4	2	2-3
4-7	4	3-4	2-3	2
(n=4)	15	3-5	2-3	2-3
	25	2-3	2-3	2
8-11	4	2-4	2-3	2
(n=5)	15	3-5	2-3	2-3
	25	2-4	2-3	2-3
12-19	4	3-5	2-3	2
(n=4)	15	4-7	2-4	2
	25	3-6	2-4	2

n = number of animals sampled

Table 3. Numbers of neurosetae present in different size classes of *Aphrodita goolmarris* n.sp.

Length (cm)	Segment number	Lower tier (no. setae)	Middle tier (no. setae)	Upper tier (no. setae)
1-3	4	3-6	2-4	2
(n=4)	15	3-7	2-6	2
	25	2-3	2	1-2
4	4	8-9	3-6	2
(n=4)	15	7-14	2-7	2-3
	25	2-4	3-4	1-2
5	4	8-9	3-6	2
(n=3)	15	10-11	5-6	2
	25	4-6	2-3	2

n = number of animals sampled

Table 4. Numbers of neurosetae present in different size classes of *Aphrodita kulmaris* n.sp.

Length cm	Segment number	Lower tier (no. setae)	Middle tier (no. setae)	Upper tier (no.setae)
3-4	4	7-9	3-5	2
(n=3)	15	12-17	4-7	2
	25	5-6	2-4	2
5-6	4	7-12	3-5	2
(n=5)	15	12-21	6-10	2
	25	6-10	3-5	2
7-9	4	5-11	3-4	2
(n=5)	15	9-19	3-8	2
	25	5-12	3-5	2

n = number of animals sampled

Table 5. Distinguishing characters of Australian and Indo-Pacific species of *Aphrogenia*.

Species name	Length (cm)	No. of segments	Elytra (pairs)	Ocular peduncles	Eyes	Median antenna	Ceratophores	Palps (extending to)	Sabre-like notosetae (elytrigerous segment)	Neurosetae	Sabre-like notosetae (cirrigerous segment)	Distribution
Aphrogenia margaritacea Augener, 1913	0.4-1.5	22-32	15 opalescent yellow/ cream	1/3 length prostomium	2 pairs	clavate, tipped, just longer than palps	2 - jointed just longer than prostomium	5, papillated	9 or more, smooth fanning across dorsum	3-4 bidentae, some with 1 extra tooth	fan of sabre notosetae arching over entire dorsum	South-eastern and South-western Australia
Aphrogenia nigropunctata Horst, 1916b	0.5-0.9	26-29	14 slightly opalescent yellow/ brown	1/2 length prostomium	absent	clavate tipped, 5x length prostomium	2-jointed 3/4 length prostomium	7-6 finely papillated	2-3 smooth fanning across dorsum	3-4, bidentate, some anterior with 1-2 extra teeth	black spot on dorsal surface of notopodia, 6 smooth setae fanning laterally	Indonesian Archipelago
Aphrogenia villosa Horst, 1916b	1.3	32	slightly opalescent tan/orange	1/2 length prostomium	1 pair	6x length prostomiun clavate tipped	1/3 length prostomium	8 papillated	6-7 shafts ridged fanning across dorsum	3, bidentate	about 10, shafts ridged, fanning laterally	Indonesian Archipelago

Table 6. Distinguishing characters of Australian and Indo-Pacific species of *Laetmonice*. * Characters defined based on figures

Species Name	Length (cm)	No. of segments	Elytra (pairs)	Eyes	Purse-like flaps on prostomium	Median antenna	Neurosetae	Ocular peduncles	Palps (extending to)	Harpoon notosetae	Distribution
Laetmonice arenifera Horst, 1916a	1.3	31	15	1 pair	absent	missing	3, fringe of short hairs on longer branch	1/3 length prostomium	10th setiger, finely papillated	2-3 recurved fangs	Indonesian Archipelago
Laetmonice batheia Horst, 1916b	2.6	33	14, covered by felt but no longer present on type	absent	absent	missing	3, fringe of hairs on longer branch	length prostomium	14th setiger, finely papillated	3 recurved fangs, shaft covered with acute tubercles	Indonesian Archipelago
Laetmonice brachyceras (Haswell, 1883)	1.2-3	34-36	15, no felt	absent	absent	2-4x length prostomium, clavate tipped	3-4, shaft smooth, or with plumose edge, some with many extra teeth	length prostomium	9-11th setiger, smooth	2-4 recurved fangs	Northern Australia, Indonesian Archipelago
Laetmonice brevihastata Ehlers, 1918	1.65	29	14	absent	?	2x length prostomium, clavate tipped	7-8, longer shaft short, fine pinnae	small	10th setiger, smooth	* 3 recurved fangs	New Guinea
Laetmonice ciridescens Horst, 1917	1.4-1.9	31-32	14-15, thin felt	absent	absent	6x length prostomium, clavate tipped	3, basal spur and distal fringe	length prostomium	12th setiger, finely papillated	3 recurved fangs	Indonesian Archipelago
Laetmonice conchifera (Horst, 1916a)	0.95	28	15	absent	absent	length prostomium, clavate tipped	2-3, bidentate with 2-3 accessory teeth	1/3 length prostomium	6th setiger, smooth	absent	Indonesian Archipelago
Laetmonice dolichoceras (Haswell, 1883)	2.5	35	15, no felt	2 pairs, faint grey	2 pairs	longer than palps, clavate tipped	3, bidentate some with 1-3 accessory teeth	length prostomium	8th setiger, finely papillated	2-4 recurved fangs many covered in sheaths	North-eastern Australia

Table 6 (cont'd).

Species Name	Length (cm)	No. of segments	Elytra (pairs)	Eyes	Purse-like flaps on prostomium	Median antenna	Neurosetae	Ocular peduncles	Palps (extending to)	Harpoon notosetae	Distribution
Laetmonice dubiosa Horst, 1916b	2.8	35	15	* present	* absent	?	fringe of hairs on longer branch	* length prostomium	* smooth, long	3 recurved fangs, smooth shaft	Indonesian Archipelago
Laetmonice malayana Horst, 1916b	1.5-4.5	30-34	15, no felt	absent	absent	3x length prostomium, blunt tipped	3-4, fringe of hairs on longer branch	2/3 length prostomium	9-10th setiger finely papillated	3-5 recurved fangs, shaft beset with thorns	Indonesian Archipelago
Laetmonice moluccana (Horst, 1916b)	0.42-3.0	20-35	15, no felt	2 pairs	absent	5x length prostomium, clavate tipped	3-4, bidentate, with 1-2 distal teeth	1/3 length prostomium	6th setiger, finely papillated	3-4 recurved fangs usually covered in sheaths	Northern Australia, Indonesian Archipelago
Laetmonice nitida Treadwell, 1926	1.5-2.2	35	15	2 pairs, dorsal and ventral pair same size	* absent	broken	bidentate with 1-4 extra teeth	* 1/3 length prostomium	8-10x length prostomium, finely papillated	3 recurved fangs	Philippines
Laetmonice parva (Horst, 1916b)	1.5	33	15	2 pairs, dorsal pair smaller	absent	3x length prostomium, clavate tipped	2-3, bidentate with 1-2 accessory teeth	length prostomium	7th setiger, finely papillated	2-3 fangs shaft covered with minute tubercles	Indonesian Archipelago
Laetmonice producta Grube, 1877	2.6-8.1	41-45	18, no felt	absent	present	2 x length prostomium, clavate tipped	3, fringe of hairs on longer branch	length prostomium	9-11th setiger, smooth	3-5 recurved fangs	South-eastern Australia
Laetmonice rugosa Horst, 1916b	1.7-3.6	32-35	15, covered by felt	absent	absent	just shorter than palps, clavate tipped	2-4, bidentate with 3-5 accessory teeth	length prostomium	8th setiger, smooth	3 recurved fangs, shaft smooth or covered with fine tubercles	Indonesian Archipelago
Laetmonice violascens Grube, 1875	1.3-2.0	33	15, pale violet	absent	?	1/3 length of palps	?	small	?	4 recurved fangs	China Sea

Table 6 (cont'd).

Species Name	Length (cm)	No. of segments	Elytra (pairs)	Eyes	Purse-like flaps on prostomium	Median antenna	Neurosetae	Ocular peduncles	Palps (extending to)	Harpoon notosetae	Distribution
Laetmonice viridescens Horst, 1917	1.4-1.9	31-32	14-15, thin felt	absent	absent	6x length prostomium, clavate tipped	3, basal spur and distal fringe	length prostomium	12th setiger, finely papillated	3 recurved fangs	Indonesian Archipelago
Laetmonice wonda n.sp.	2.4-4.1	34-35	15, no felt	2 pairs, pale greys	present	missing	3, fringe of hairs on longer branch	1/4 length prostomium	13th setiger, finely papillated	3-4 recurved fangs on some shafts with tubercles	South-western Australia
Laetmonice yarramba n.sp.	1.7-4	29-34	13-15, no felt	absent	absent	5x length prostomium, blunt tipped	3-4, fringe of hairs on longer branch	1/3 length prostomium	9-11th setiger, finely papillated	3 recurved fangs, some shafts with tubercles	Eastern and western Australia

Table 7. Numbers of notosetae present in different size classes of *Laetmonice malayana*.

Length (cm)	Elytrigerous segment number	Number of neurosetae	Number of notosetae (acicular)	Number of notosetae (harpoon)*
1-2	5	2-3	6-8	2-4
(n=2)	15	3-4	7-11	3-4
	25	2	6-7	2
2.1-3	5	3	6-12	3-9
(n=5)	15	3	10-18	3-6
	25	3	6-14	3-6
3.1-4	5	3-4	8-12	6-9
(n=4)	15	3	12-14	5-7
	25	3	10-13	4-5
4.1-5	5	3-4	7-12	3-6
(n=5)	15	3	11-16	4-5
	25	3-4	7-14	2-4

n = number of animals sampled

* Where harpoon notosetae were missing setal scars were counted.

Table 8. Numbers of notosetae present in different size classes of *Laetmonice producta*.

Length (cm)	Elytrigerous segment number	Number of neurosetae	Number of notosetae (acicular)	Number of notosetae (harpoon)
4.1-5	5	3	16	7
(n=2)	15	3	10-15	4-7
	28	3	12-18	4
5.1-6	5	3	10-15	6
(n=3)	15	3	12-19	9-10
	28	3	8-12	6-8
6.1-7	5	3	14-20	4-11
(n=3)	15	3	11-28	7-9
	28	3-4	17-20	5-8
7.1-8	5	3-4	17	4-6
(n=2)	15	3	17-22	9-12
	28	3	14-16	7

n = number of animals sampled.

Note. Although many *L. producta's* were available for examination, the majority were missing both their harpoon and acicular notosetae. Due to their large size, numbers of harpoon notosetae could be determined by the presence of setal scars, however the acicular notosetae being smaller left no setal scars. As a result only specimens that had sufficient acicular notosetae remaining along the body could be sampled.

Table 9. Distinguishing features of McIntosh, 1885 varieties of *Laetmonice producta*.

Species Name	Greatest length (cm)	Number of segments	Nuchal flaps	Ventral surface	Eyes	Palps	Elytra no. of pairs	Notosetae	Neurosetae	Distribution
L. producta	5	44-47	present	papillated	1 pair	minutely papillated	20	shafts minutely tuberculated, 5-6 recurved fangs	thick pinnae	Southern Indian Ocean
L. producta var. *wyvillei*	4.3	43	present, small	thickly papillated	absent	finely papillated	18	shafts thickly tuberculated, 3-4 recurved fangs	pinnae slender, numerous, elongate	Southern Indian Ocean, southern Atlantic Ocean
L. producta var. *benthaliana*	4.8	33	present, small	smooth	absent	finely papillated	15-18	shafts with small tubercles and fine hairs, 3-4 recurved fangs	pinnae, fine, short	Southern Indian Ocean, northern Pacific Ocean
L. producta var. *willemoesi*	3.3	35	absent	finely papillated	absent	papillated	15	shafts with many prickles, 3-4 recurved fangs	pinnae long, slender, spur sometimes bifid	Northern and southern Atlantic, southern Indian Ocean, northern Australia and New Zealand.
L. producta var. *assimilis*	3.5	35	absent	papillated	absent	papillated	15	shafts smooth, 3-4 recurved fangs	pinnae long, slender	North Atlantic Ocean

Table 10. Distinguishing characters of Australian and Indo-Pacific species of *Pontogenia*.

Species name	Length (cm)	No. of segments	Ocular peduncles	Eyes	Median antenna	Palps (extending to)	Length of median ceratophore	Paleal Notosetae	Neurosetae	Felt	Distribution
Pontogenia araeoceras (Hawsell, 1883)	0.16-2.5	14-46	length prostomium	1 pair	1 length palps tapered articulate tip	6th setiger, finely papillated	just longer than prostomium	23, tuberculated	3-4, bidentate	present	Northern Australia
Pontogenia indica Grube, 1875	2.6	43	short	?	more than 5x length of prostomium	finely papillated	?	curved, with sub-terminally tooth, 18	3-4, bidentate	?	Philippine Islands
Pontogenia macleari (Haswell, 1883)	0.9-4.3	29-39	3/4 length prostomium	1 pair	2x length prostomium	5th setiger, finely papillated	just shorter than prostomium	10-25 denticulated, giving serrated appearance	2-4, bidentate	present	Eastern Australia, Indonesian Archipelago
Pontogenia spinosa Horst, 1917	2.5	35	2/3 length prostomium	2 pairs	3x length prostomium clavate tipped	5 setiger smooth	2/3 length prostomium papillated	25 with long spines on each edge	3-4, bidentate	present	Indonesian Archipelago
Pontogenia villosa Horst, 1917	2.4	34	length prostomium	2 pairs	broken	finely papillated	2x length prostomium papillated	14 with small denticles	4, bidentate	present (thick)	Indonesian Archipelago

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